

# The Behavioural Profile of *Pongo pygmaeus morio* in Kutai National Park: Positional Behaviour In a Precarious Habitat

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## Abstract

This study examined the positional behaviour of female *Pongo pygmaeus morio* individuals in Kutai National Park, East Kalimantan, Indonesia during the 2015-2016 El Niño cycle. Several positional behaviour studies have been conducted on the Sumatran orangutan (*P. abelii*), yet only one had been conducted on *P. p. morio*; this study was conducted by Cant in 1982, during a similarly strong El Niño cycle, and also only sampled female individuals (1987a). As such, this study provided an opportunity to verify the behavioural profile of *P. p. morio* as found by Cant during a similar environmental year, as well as verify the interspecific comparisons drawn from his sole study 35 years ago. This study verified some of the previous interspecific findings – mainly that *P. p. morio* employs an elevated use of ‘ipsilateral suspend’. However, some divergences from previous findings were found – mainly that ‘brachiation and forelimb swing’ and ‘sway’ occurred at higher frequencies than previously found in *P. p. morio*. Lower levels of ‘vertical climb’ and ‘descent’ were also found in *P. p. morio* here than found in the previous *P. p. morio* study.

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## **Foreword**

My aim in pursuing a Masters in Environmental Studies was to study wildlife in the anthropocene. I was presented with the opportunity to study great apes, and I hoped to explore the scientific, educational, and creative approaches employed to aid in their conservation, as well as to explore the main factors impacting their populations and habitats.

As per my POS, through courses, I developed an understanding of current topics and research methods in the conservation field, and I examined the synergistic effects of anthropogenic and environmental pressures. Further, I explored human-animal relationships, and gained an understanding of great ape behavioural ecology and habitat requirements.

Conducting this research in Kutai National Park, however – where all of these issues seem to coalesce and the impact of anthropogenic pressures is undeniably clear – was perhaps the most educational and impactful experience. I believe the combination of MES courses taken and this field research achieved the goals I set out in my Plan of Study.

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## Chapter 1 – Introduction

Today, 60% of primate species are officially at risk of extinction, and 46% of tropical forests are now fragmented due to deforestation practices (Estrada et al., 2017). Due to anthropogenic pressures such as habitat loss, fragmentation, hunting, and extractive industries – all extant great ape species are now formally classified as Endangered or worse (Schoneveld-De Lange et al., 2016; IUCN, 2016a).

The Sumatran orangutan became Critically Endangered in 2008, and the Bornean orangutan was recently upgraded to Critically Endangered in 2016 (IUCN, 2016b). Currently, 75% of orangutans live outside of protected areas (Meijaard et al., 2011), and those living within protected areas are suffering the repercussions of poorly enforced boundaries; the global demand for natural resources found within park boundaries is considered to be the main culprit (Schoneveld-De Lange et al., 2016; Moeliono and Purwanto, 2008; Meijaard et al., 2011).

This study took place in Kutai National Park, East Kalimantan; a severely degraded landscape (Wich et al., 2008), with an estimated \$USD 92 billion worth of coal within its park boundaries (Limberg et al., 2009). However, as one of the last lowland dipterocarp orangutan habitats, it is an important ecosystem for continued research (Russon et al., 2015). In Kalimantan, orangutan population decline is being exacerbated by human encroachment, habitat loss resulting in human-orangutan conflict, the growing wildlife trade, and increasing accessibility to forests often resulting from roads built for extractive industry purposes (Schoneveld-De Lange et al., 2016; Corlett, 2007; UNEP, 2002). Additionally, the impact of climate change and the increasing severity of El Niño Oscillation Events (ENSO) may force primates out of their home ranges, leading some to venture out of protected areas, which is likely to negatively affect populations that are already declining and at risk (Estrada et al., 2017). However, ecological and habitat resilience has been identified in *Pongo pygmaeus morio* (Estrada et al., 2017; Russon et al., 2015), and examining the parameters of their resiliency may be a crucial aspect to informing conservation practices and population projections.

With these components in mind, this study sought to study the behavioural profile of KNP's female orangutans, specifically by sampling the positional behaviour employed within their habitat. A main goal was to repeat Cant's study, conducted 35 years ago (1987a), to provide

a more robust representation of *P. p. morio*'s behaviour in KNP. Further, however, this study sought to examine the behavioural profile of female individuals amongst their increasingly delicate habitat, as female orangutans have been found to be the first and foremost affected by various disturbances (Hardus et al., 2012).

## Chapter 2 – Literature Review

### 2.1 Importance and interest in positional behaviour

#### 2.1.1 *Evolutionary morphology*

Primates have the widest range of locomotor adaptations to living arboreally of all the vertebrates (Mcgraw and Sciulli, 2011), and positional behaviour in arboreal living primates - studied for over a hundred years - became a rigorous topic of research in the 1960's (Hunt et al., 1996). Importantly, positional behaviour studies have the potential to inform evolutionary postcranial morphology in hominoids (all members of Hominoidea, including all extant great apes and humans) as an arboreal clade (Grehan and Schwartz, 2009; Thorpe and Crompton, 2006; Cant, 1987a).

Orthograde orientation (an upright torso) in arboreality is considered to be the common denominator among the great apes (Myatt et al., 2011; Crompton et al., 2008), and characteristics common across great apes such as broad torsos, arms with the ability to raise overhead, and a scapula on the dorsal side are all considered to be locomotor traits that confirm their common arboreal origins (Thorpe and Crompton, 2006).

There are several features of orangutan morphology studied that have been considered to be fundamental to facilitating their life in the trees with the heaviest bodies of all arboreal species (Cant, 1987a). Such studies have proposed hypotheses suggesting arboreality necessitates suspension from the forelimbs leading to the longer forelimb adaptation, and shorter hindlimbs are hypothesized to have evolved to allow their heavy bodies to maintain balance above substrates when travelling through the canopy (Cant, 1987a).

#### 2.1.2 *Habitat and ecological correlates*

The orangutan (*Pongo*) is Asia's only extant ape, and is now recognized as comprising two species – surviving in various degrees of 'wildness' in Borneo (subspecies: *pygmaeus*, *morio*, and *wurmbii*) and Sumatra (*abelii*) (Wich et al., 2008). Figures from 2008 found approximately 6,500 *P. abelii* in Sumatra (classified by the IUCN red list as Critically Endangered in 2008 (IUCN, 2016), and 54,000 *P. pygmaeus* remain in Borneo (Wich et al., 2008). Based on

estimates reported from the most recent census, the Bornean orangutan was upgraded to Critically Endangered in 2016 (IUCN, 2016).

In Borneo alone, orangutan habitats range greatly – including lowland dipterocarp forests, peat swamp forests, and freshwater forests, varying on the spectrum from primary to secondary forests (Manduell et al., 2011; Wich et al., 2008). *Pongo pygmaeus morio* is found only in East Kalimantan and Sabah (Malaysia); approximately 4,800 individuals remain in Kalimantan, and approximately 15,000 in Sabah (Wich et al., 2008). *Pygmaeus* is found in northwest Borneo at an estimated 3000-4,500 individuals, and *P. p. wurmbii*, found in Central Kalimantan, has an approximate 30,000 individuals remaining (Wich et al., 2008).

Habitat and ecological conditions impact orangutan arboreal behaviour, as habitats vary in the availability and compliancy of substrates, and studies have found stronger associations between certain substrates and positional behaviours than others (Thorpe and Crompton, 2005; 2006; 2009). This finding suggests that orangutans select for certain substrates as a solution for the arboreal problem presented (Thorpe and Crompton, 2006; 2009). Studying orangutan positional behaviour, then, has the potential to provide great insight into critical linkages between their behaviour and habitat, and forest quality (Manduell et al., 2011).

### *2.1.3 Negotiating precarious habitats*

Arboreality is accompanied by a variety of challenges for primates; acquiring preferred foods on terminal and thus very compliant branches, predator avoidance, fleeing from conflict, and efficiently navigating and travelling through a canopy that can change abruptly and is characterized by wide gaps that require complex locomotor and postural solutions (Mittermeier and Fleagle., 1976; Myatt et al., 2011). While negotiating an arboreal lifestyle presents challenges regardless of the primate's body size and weight, orangutans face the greatest challenges as the heaviest predominantly arboreal primate (Cant, 1992); adult females weigh 39 kg on average, and adult males roughly double that weight (Knott and Kahlenberg, 2011; Cant, 1987a; Rodman, 1984). As such, orangutans arguably bear a greater burden in arboreal negotiation than other arboreal primates, and much of the interest in orangutan positional behaviour arises from the fact that they are the largest arboreal primate, and navigating an

arboreal lifestyle only becomes more challenging and precarious as body size and weight increases (Thorpe and Crompton 2009; Myatt et al., 2011).

Cant (1992) illustrated the main issues orangutans must mediate daily concerning their arboreality – managing larger support substrates (i.e. tree trunks with wide circumferences), bridging gaps in the canopy, increasing their efficiency (i.e. more direct pathways), and increasing the speed of travel along arboreal pathways.

Negotiating routes to solve some of the most important problems affecting survival – securing resources, acquiring mates, fleeing conflict, avoiding predation – most likely requires an elevated capacity for problem solving. Povinelli and Cant (1995) proposed that orangutans might possess a mental capacity they named ‘self conception’, developed from the need for heavy bodied mammals to cope with the obstacles and complexity of their fragile environment which is compliant under their weight. For them, self-conception is: “...an awareness of the self as (1) an object of knowledge, (2) the subject of experience, (3) an entity that exists through time, and (4) a causal agent” (1995, pg. 393). They argued that, as orangutans must plan and execute unusual locomotion flexibly in arboreality to accommodate their heavy weight in a precarious and uncertain habitat, they must possess a degree of ‘self conception’ because it is necessary to determine viable locomotor and postural solutions to the continual issues posed by arboreality.

Examining the positional behaviour of the orangutan therefore has the potential to illuminate a broad array of solutions employed by the last arboreal great ape. These findings not only have implications for evolution, but also perhaps for the orangutan’s behavioural flexibility. Orangutan habitats are shifting – forest loss, degradation, conversion, and the move towards human-dominated landscapes – and information on how well they cope and adjust may be crucial to appropriate conservation planning (Campbell-Smith et al., 2011).

#### *2.1.4 Positional behaviour studies*

Orangutan positional behaviour was initially described qualitatively in narrative form - such as by Wallace (1869) and Davenport (1967) (Thorpe and Crompton, 2009). Sugardjito (1982) started the tradition of sampling positional behaviour in orangutans quantitatively. The studies included in the comparison to follow are listed here.

***P. abelii***. Sugardjito and van Hooff (1986) collected data from 128 full-day (dawn-to-dusk) focal individual follows over two and a half years in Gunung Leusure National Park, Sumatra, Indonesia. They used bout sampling to measure locomotor modes during *travel*, and postural modes during *rest*. Thorpe and Crompton calculated pauses during *travel* for their study, and included them in the tables found below in this paper (Table 8). This study's focal individuals included all age-sex classifications. Thorpe and Crompton (2006; 2009) collected data from 97 full-day focal individual follows, over the course of 13 months also at the Ketambe Research Station, and employed instantaneous sampling on the one-minute mark. They measured postural modes during *travel*, *feed*, and *rest*, and locomotor modes during *travel* and *feed*. Their study's focal individuals included all age-sex classifications. Cant (1987b) collected data on postures during *feed* in a short-term study during a fruit period of about 8 days, also at the Ketambe Research Station. His study included one male and one female.

***P. p. morio***. Cant (1987a) collected data over a 4-month study, on two adult females for 28 full day focal individual follows. He measured locomotor modes (weighted in distance) in *feed* and *travel*, as well as postural modes (weighted in minutes) during *feed*. This study took place in Kutai National Park, East Kalimantan, Indonesia. The current study is the second on *P. p. morio*.

#### *2.1.5 Classifying primate positional behaviour*

In 1965, Probst wrote that the classification of primate positional behaviour was “in disarray” (Hunt et al., 1996, p. 363). There have since been efforts to remedy the inconsistencies in terminology and categories (Hunt et al., 1996). In 1996, Hunt published a standardization for positional behaviour that emphasized a biomechanical perspective and provided 32 modes, further subdivided into sub-modes; 52 postural and 74 locomotor (Hunt et al., 1996).

Thorpe and Crompton (2006) undertook analyzing the results across available orangutan-specific positional behaviour studies to date. Due to the methodological differences across those studies, Thorpe and Crompton sought to clarify and consolidate positional behaviour modes into a simpler, broad based system that enabled interspecific comparison. They created a compromise classification table that conflated many modes while maintaining important distinctions such as weight bearing limbs and torso orientation. It consists of eight locomotor modes and nine postural modes that are suitable for interspecific comparison (descriptions provided in Methods,

below). It remains the most recent refinement to positional behaviour classification, and because Thorpe and Crompton reworked previous positional behaviour data, it allows for interspecific comparison as well as comparisons across sites and over time within sites.

#### *2.1.6 Kutai National Park*

New study of positional behaviour in KNP is valuable for several reasons. There is scarce suitable habitat left for orangutans, and KNP is one of the last lowland dipterocarp orangutan habitats (Russon et al., 2015). As Cant conducted the only other positional behaviour study on *P. p. morio* in KNP in 1982, repeating his study has the potential to provide insight into adaptations and adjustments to damaged habitat. KNP is considered severely degraded (Wich et al., 2008), yet a large portion of remaining *P. p. morio* in East Kalimantan survives there, which speaks to the known resiliency of *P. p. morio*, as well as the importance of this habitat (Russon et al., 2015).

Examining the various forms in which their resiliency manifests itself might reveal important behavioural flexibilities and their limits, as well as inform future suitable conservation planning for this subspecies in this protected area of habitat. The trajectory of habitat degradation in KNP is only expected to continue in its current direction - further habitat encroachment, degradation, and fragmentation (Moeliono and Purwanto, 2008). Studying orangutan behavioural responses to habitat change is a crucial component of conservation, and not many studies have examined these responses (Hardus et al., 2012; Russon et al., 2015). This study provided an opportunity to do so.

#### *2.1.7 Knowledge gap*

The only comprehensive study thus far that compares the positional behaviour of Sumatran (*P. abelii*) and Bornean (*P. p. morio*) orangutan species' positional behaviour is that of Thorpe and Crompton (2009). Their study identified the interspecific differences in positional behaviour between *P. abelii*, and *P. p. morio*, using the compromise classification table and the data available at the time. Accordingly, their information about *P. p. morio*'s behavioural profile was derived from a single study – Cant (1987a). As such, a new study has the potential to verify

or show divergences from the interspecific comparisons drawn by Thorpe and Crompton (2009). Further, Cant collected postural behaviour only during the behavioural context of *feed* – so no interspecific comparison is available for postural modes during *rest* and *travel*. This study was able to collect that data and fill that knowledge gap. Finally, Cant’s study (1987a) was conducted in KNP during the 1982 -1983 El Niño event, and observed only female individuals – both of which have been described as limitations to his study (Thorpe and Crompton, 2009). Conducting a new positional behaviour study in the same national park (KNP) during an El Niño event of similar strength (Null, 2017), and on a similar data set of individuals provides the opportunity to examine behavioural changes over time.

#### *2.1.8 Research questions*

The aim of this study was twofold. Firstly, as there has only been one previous study sampling the positional behaviour of *P. p. morio* (aged 35 years), a primary aim of this study was to examine and verify the positional behaviour of Bornean orangutans in KNP, East Kalimantan, Indonesia. Conducting this study contributed to the creation of a more robust and representative profile for *P. p. morio*’s positional behaviour.

Secondly, this study aimed to examine the interspecific comparisons between *P. abelii* and *P. p. morio* that have been concluded based on Cant’s sole study.



## Chapter 3 – Methodology

### 3.1 Field Study Area

This field study took place in Kutai National Park (KNP) ( $0^{\circ} 05' - 0^{\circ} 35' \text{N}$ ,  $116^{\circ} 55' - 117^{\circ} 35' \text{E}$ , 0-258 m a.s.l), East Kalimantan, Indonesia (Figure 1). The government of Indonesia established KNP as a national park in 1982 (Setiawan et al., 2009; Campbell, 1992), and it had been classified as a nature reserve in 1936 by the Sultan of Kutai and protected as such. Originally a combination of primary mixed dipterocarp and riparian forest, it has experienced over the years, and continues to experience, many environmental and anthropogenic pressures. Approximately 199,000 ha in area of KNP was severely damaged by severe drought and forest fires in 1982-83 and 1997-98 (Yeager et al., 2003; Russon et al., 2015); by the end of 1998, and only 5% of KNP's forest was left (Setiawan et al, 2009; Meijaard and Nijman, 2000).

Figure 1. Map of Kalimantan with KNP highlighted (Yeager et al., 2003)



KNP is now recovering as a combination of primary and secondary lowland riverine to upland dipterocarp forest (Russon et al., 2015). Some areas of KNP have periodically been logged since the 1970's (Rayadin and Saitoh, 2009). KNP is also adjacent to and suffers degradation from the biggest coalmine in the East Kutai region of East Kalimantan, Prima Coal (KPC) (Setiawan et al, 2009). It is also surrounded by nickel mining, pulp and paper and palm oil plantations, a timber concession, and is subject to encroachment from hunters, illegal human settlement, and illegal loggers (Setiawan et al., 2009, Meijaard et al., 2010). Given the vast amount of biodiversity in KNP, and that many of its species are of at least endangered status, this forest is an important location for further research as it may inform conservation planning moving forward (Russon et al., 2015; Moeliono and Purwanto, 2008). Primatological and ecological studies have been conducted in this park periodically since the 1970s (Campbell, 1992), so there is a considerable amount of published data with which to compare and analyze new data.

The Prefab research station area (00 ° 31' 54.6 ° N, 117 ° 27'54. 0"E) was chosen for this study (Figure 2), because it is well established and it was regularly used by orangutans in 2015 despite the serious drought conditions (A. Russon, personal communication, May 1 2015). The Prefab was developed and utilized for primatological research by Dr. Akira Suzuki of Kyoto University between the years of 1988 – 2015. It had previously been mapped for a basic transect system and some individual trees had been identified and labeled for research purposes. In 2015, the KNP authorities authorized research activities at this location by Dr. Anne Russon of York University, who also operates the Orangutan Kutai research project (Project OK) at the Mentoko research site (00 ° 34'04.0", 117° 25'53.0"E), located approximately 10 kilometers upriver. This study was conducted as part of and in conjunction with Project OK, which studies orangutan diet, activity budgets, and feeding ecology (Russon et al., 2015).

Figure 2. Map of KNP, with Prefab and Mentoko research sites highlighted (Setiawan et al., 2009)

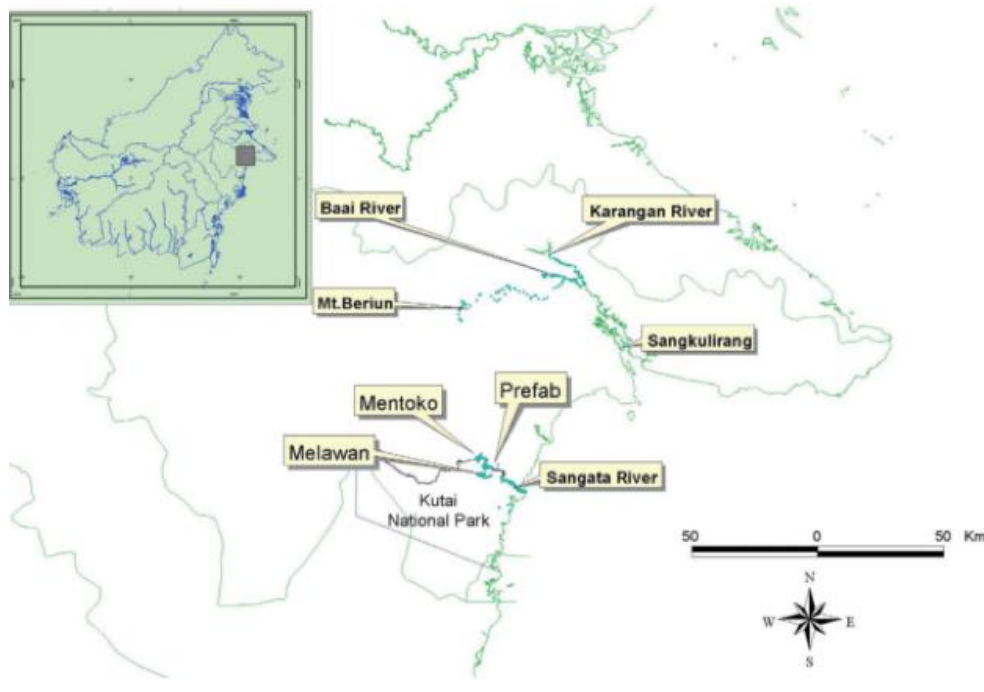
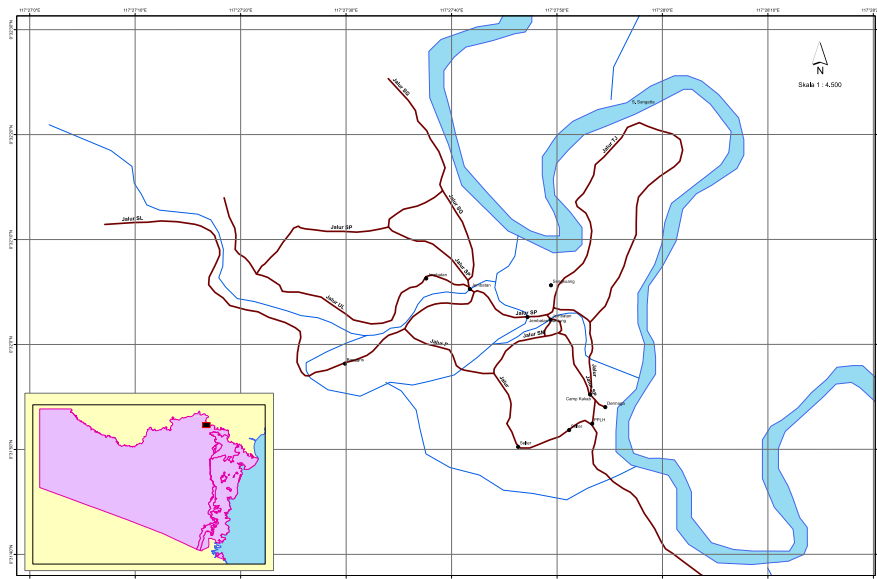


Figure 3. Prefab site transect system map (Project OK, 2015)



### 3.2 Study Individuals

Five female individuals were observed throughout the months of July 2015, December 2015, and January 2016 (Table 1). This split scheduling resulted from a delay in the foreign research permit application process.

Following Wich et al.'s age-sex classifications (2004), this study observed three adult females (two reproductively active, one “elderly”), one juvenile, and one adolescent. The two reproductive adults (Labu, Bayur) were observed both while pregnant and post-pregnancy with their clinging infants (Labu also had a dependent juvenile throughout). Thorpe and Crompton (2005) suggested noting when an infant was clinging or travelling independently as Sugardjito and van Hooff (1986) found that the locomotor repertoires of the mothers they observed changed after giving birth. The juvenile female, Langit, was still travelling with her mother Labu although she often made and used her own nest nearby; she displayed no sexual activity. The adolescent female, Ulin, was entirely independent but not yet reproducing. Finally, the “elderly” adult female is Tanjung; she is 50+ in age and sexually active throughout the duration of this study. Although at which point an ape becomes “elderly” is not agreed upon, the current life expectancy of wild female Bornean orangutans is approximately 53 years of age (Wich et al., 2004; Lowenstine et al., 2016),

The orangutans that range within the Prefab site have been studied for over 30 years, and are an attraction for “ecotourists”, so they are well habituated to observers. The females I observed rarely demonstrated agitation by or aggression towards human observers, and remained in view; hiding behaviour was almost never observed. They are also well known to long-term local Prefab research assistants, who were able to provide accurate ages and lineages. Further, collaborating with long-term Prefab research assistants ensured proper recognition of individuals.

Table 1. Individuals - observed during the months of July 2015, December 2015, January 2016<sup>1</sup>

Name	Age-sex category	Age	Notes
Labu	Pregnant adult female	ca. 28	Observed while pregnant during December 2015 - travels with juvenile daughter
Labu	Adult female	ca. 28	Adult female with clinging infant - travels with immature Langit
Langit	Juvenile female	5	Eldest daughter of Labu - travels with mother, often makes and sleeps in own nest
Luna	Infant female	3-4 months	Daughter of Labu - clinging infant - born in October of 2015
Bayur	Pregnant adult female	ca. 27	Observed while pregnant during December 2015 - displayed dominance over Labu
Bayur	Adult female	ca. 27	Adult female with clinging infant
Baby <sup>2</sup>	Infant	0-2 months	Daughter of Bayur - clinging infant - born January 1st of 2016
Ulin	Adolescent female	ca. 9	Independent - travelling with unknown sub-adult male during observation days
Tanjung <sup>3</sup>	Adult female	50+	Mother of Bayur - grandmother to 'Baby' - sexually active during study period

<sup>1</sup> This table includes two infants who were not focal individuals but are included here as it may be possible that they influence the positional behaviour of their mothers

<sup>2</sup> As we had yet to determine the sex of Bayur's infant, we simply named him/her 'Baby' for the time being

<sup>3</sup> Only one day of positional behaviour data was collected for Tanjung - all other days we encountered her, we observed her interesting interactions with her pregnant daughter

### 3.3 Measures

#### *3.3.1. Definitions*

Thorpe and Crompton (2009) followed the definitions for positional behaviour outlined by Hunt (1996), and established by Prost in 1965; positional behaviour includes posture and locomotion. As Thorpe and Crompton published the most recent interspecific comparison on orangutan positional behaviour and I use their compromise classification table, I employed their definitions in this study. Postural behaviour was recorded when the individual's body mass remained "in a relatively stable relationship with its environment and adjustment of body parts (e.g. appendages) occur" (Cant, 1987a, p. 77). Locomotor behaviour was recorded when the individual's mass changed location (Cant 1987a). Per Thorpe and Crompton's (2009) compromise classification table, postural behaviour includes 9 modes, and locomotor behaviour includes 8 modes. Mode descriptions are provided in Tables 2 and 3, below.

The original tables, as they appear in Thorpe and Crompton (2009), can be found in Appendix 1. For a detailed account of how the compromise classification table was created, see Thorpe and Crompton (2006).

#### *3.3.2. Recording positional behaviour*

Postural and locomotor behaviour was recorded during the behavioural contexts of resting, traveling, and feeding. The unit of observation for both postural and locomotor behaviour was a 'bout' of time defined by a single behavioural context. A bout began when any of the three behavioral contexts above began and continued until it changed; during the intervening minutes all positional behaviour that occurred was recorded.

#### *3.3.3. Behavioural contexts*

Rest was recorded when the focal orangutan employed a postural mode for more than 30 seconds (i.e., did not move) and was not eating or engaging in other activity. Travel was recorded when the focal orangutan employed a locomotor mode to change trees, either arboreal or terrestrial; if the individual employed locomotor modes to move within a tree's canopy while feeding, that was considered a feeding event, not travelling. Feed was recorded when the focal

orangutan engaging in any feeding behaviour; this includes the reaching for, processing, or chewing a food item.

Bouts of behavioural context were recorded in minutes; all positional behaviour that occurred within a bout (or as much as was visible amongst the canopy) was recorded. For example, if an individual was feeding from 12:00 pm to 12:05 pm, all positional behaviour modes, both locomotor and postural, that occurred during this feeding bout were recorded. The bout ended when the individual began to exhibit a different behavioural activity (e.g. finished eating and began travelling). Further positional behaviours were then recorded as occurring during the subsequent behavioral context (e.g., travelling). This system allowed for continuity with Project OK's established data collecting method. Utilizing the same observation sheets as the Project OK research assistants while following the same focal individuals each day allowed for activity data to be consistent and useful for both parties.

Table 2. Positional behaviour classifications - postural modes <sup>1</sup>

Modes	Description
1. Sit	recorded when orangutan is sitting with weight on ischia. This posture was either subcategorized as "assisted" or "unassisted", by the forelimbs, or "other" if unclear
2. Pronograde stand	recorded when orangutan's torso is pronograde in orientation, and is standing on either 3 or 4 limbs
3. Orthograde stand	recorded when orangutan's torso is orthograde in orientation, and is standing on either 1 or 2 hindlimbs
4. Orthograde forelimb-suspend	recorded when orangutan's torso is orthograde in orientation, and is suspended by forelimbs that are bearing body mass
5. Orthograde quadrumanous-suspend	recorded when orangutan is in suspensory posture whereby hindlimbs and forelimbs bear weight of body mass
6. Forelimb-hindlimb suspend	recorded when orangutan is either ipsilaterally (same side of the body) or contralaterally (opposite sides of the body) suspended from one hindlimb and one forelimb
7. Pronograde suspend	recorded when orangutan is suspending from both forelimbs and hindlimbs, torso inverted and pronograde in orientation
8. Hindlimb suspend	recorded when orangutan is using either one or both hindlimbs to suspend upside down
9. Lie	recorded when orangutan is lying with weight supported by back or stomach

<sup>1</sup> These modes are based strictly on Thorpe and Crompton's (2009) *compromise classification table* for positional behaviour

Table 3. Positional behaviour classifications - locomotor modes <sup>1</sup>

Modes	Description
1. Quadrupedal & tripedal walk	recorded when individual engages in tripedal and quadrupedal gait, either irregular or regular
2. Torso-orthograde suspensory locomotion	recorded when an individual engages in suspensory locomotive modes whereby forelimbs mainly support body mass and torso is orthograde in orientation
3. Bipedal walk	recorded when an individual's torso is orthograde in orientation, and the hindlimbs support and propel locomotion (either assisted or unassisted by the forelimbs)
4. Torso-pronograde suspensory locomotion	recorded when an individual's torso is orthograde in orientation, and the hindlimbs support and propel locomotion (either assisted or unassisted by the forelimbs)
5. Bridge	recorded when an individual crosses a gap with torso pronograde in orientation
6. Vertical climb	recorded when an individual climbs vertically – which is considered here to be within 20 degrees of true vertical, or is considered angled climb when between 20 degree-45 degrees
7. Vertical descent	recorded when individual descends vertically – which is considered here to be mirroring the constraints of vertical/angled climb, as above
8. Sway	recorded when an individual engages in oscillatory locomotive movement – this includes 'tarzan style' swinging and tree swaying

<sup>1</sup> These modes are based strictly on Thorpe and Crompton's (2009) *compromise classification table* for positional behaviour

### 3.3.4. Methodological differences

While a priority of this study was to repeat Cant's KNP study as closely as possible, some differences in methodologies inevitably occurred.

First, Cant weighted locomotor bouts by distance during *travel* and *feed*, and weighted postural bouts during *feed* by time in minutes. He did not record postural behaviour during *rest* or *travel*. This study, however, weighted all bouts within all behavioural contexts by time in minutes, to follow the trajectory of positional behaviour studies post-Cant (see Thorpe and Crompton, 2006; 2009).



Second, Cant noted and measured substrates used during positional behaviour (i.e. tree, liana, or branch), recording diameter, angle, quantity, and tree zones. These measures fall outside the scope of my study, and so were not recorded.

Third, Cant differentiated between travelling and crossings, where crossings were specific to travel across gaps between trees. In keeping with Thorpe and Crompton's recent positional behaviour studies, which have not differentiated between the two, and because analysis of gap crossing is not a focus of this study, I did not differentiate between these two items.

### 3.4 Data Collection

#### *3.4.1. Data Sampling*

Orangutans, who are semi-solitary, are notoriously difficult to locate and can be hard to follow, as they can be very quiet (even when travelling) and can be hard to spot due to poor visibility through the canopy. Therefore, the individuals used as subjects in this study are those that the author and small team of local research assistants (minimum 2, maximum 4), were able to locate by searching the research area and subsequently follow. This is standard procedure in studies of wild orangutan behaviour.

The observational data for this study were obtained during nest-to-nest focal orangutan follows (ca 6 am - 6 pm, from rising in the morning to resting for the night). Cant (1987a) split the observational day between himself and a research technician, each collecting a half-day's data. I normally observed orangutans for complete days, from nest to nest, unless illness or other camp responsibilities required me to collect only part day data. I searched for and followed focal individuals with the help of a small team of local research assistants at Project OK. We travelled together throughout the day; they collected their standard behavioural and ecological data for Project OK's purposes while I collected data specific to this study, and they identified items such as tree and food species for me when required.

Within a nest-to-nest follow, continuous event sampling (all-occurrence) was employed for collecting and recording data. This method is often deemed most appropriate for measuring the frequency of target events, in this case the frequency of positional behaviour modes (Martin

and Bateson, 2007). Data were recorded and coded manually with pen and paper on the pre-formatted data coding sheets used by Project OK. The behavioural information recorded is shown in Table 4, below. An example of the data sheet used in this study is in Appendix 2.

*Ad libitum.* While the main data analyzed here consisted mainly of positional behaviour codes, qualitative ad libitum notes in narrative form were recorded extensively throughout the observation day to provide further behavioural details. Ad libitum data included descriptions of social interactions, conflicts, sexual activity, prenatal and postnatal awareness and grooming, and perceived communication between individuals.

#### *3.4.2. Training*

I self trained thoroughly and frequently for several weeks in Thorpe and Crompton's (2009) modes before the start of formal data collection and practiced regularly throughout the duration of this study. No assistants were available to collect this data with me, so inter-observer reliabilities are not an issue. I collected all positional behaviour data.

#### *3.4.3. Ethics*

As per the Ontario Animals for Research Act, 1968-69, implemented by the Ontario Ministry of Agriculture and Food, the Canadian council on Animal Care (CCAC), and the Animal Industry Branch (the Ministry), I took and passed the Animal Care Committee Protocol course administered by the Animal Care Committee (ACC) at York University prior to commencement of this study. Also, as per the CCAC recommendations, I obtained the Hepatitis A and B, typhoid, measles, rabies, polio, and influenza vaccinations prior to starting this study and prior to being in the vicinity of wildlife. Once the above requirements were fulfilled, I received York University's ACC ethics approval for this study. Finally, this study complied with and adhered to all regulations and restrictions set by the Indonesian authorities, such as RISTEK (Department of Research and Technology) and the Head of Kutai National Park (Kepala Balai Taman Nasional Kutai), and was formally authorized by all responsible Indonesian authorities.

Table 4. Data recorded during observational day <sup>1</sup>

Data Recorded	Description
1. Date	
2. Focal Individual	Including name, age, and accompanying dependents and/or companions (i.e. independent adolescents following adult females)
3. Time	the start and end time of each activity was recorded (feed, rest, or travel), and the modes observed during each of these time periods was recorded; all occurrence sampling
4. Positional behaviour	recorded using the <i>compromise classification table</i> for positional behaviour, created by Thorpe & Crompton (2009). Positional behaviour includes postural and locomotor behaviour. Postural behaviour was coded as either sit, pronograde stand, orthograde stand, orthograde forelimb-suspend, orthograde-quadrumanous suspend, forelimb-hindlimb suspend, pronograde suspend, hindlimb suspend, or lie. Locomotor behaviour was coded as either quadrupedal & tripedal walk, torso-orthograde suspensory locomotion, torso-pronograde suspensory locomotion, bipedal walk, bridge, vertical climb, vertical descent, or sway
5. Support type	Branch or liana (single or multiple), or tree trunk
6. Energetic data	Start and end times of all feeding, travelling, and resting events
7. Dietary data	Food species, food type, and food part processed and/or consumed

<sup>1</sup> Please note - not all data collected was able to be analysed in time to be included in the results and analysis of this study

### 3.5 Statistical Analysis

Thorpe and Crompton reworked the data of the previous positional behaviour studies seen in the results tables in this study to allow for comparison (interspecifically and between study sites), and presented the relative frequencies of each postural and locomotor mode in percentages by behavioural context. I calculated and presented my findings following Thorpe and Crompton (2009). For example - to find the percentage of time all study individuals cumulatively exhibited ‘quadrupedal and tripedal walk’ during the behavioural context of feed – the frequency by which all individuals exhibited this mode during feed was calculated (65 instances) and divided by the frequency total for all locomotor mode instances observed during feed (307). The relative

frequency (percentage) exhibited for ‘quadrupedal and tripedal walk’ by all study individuals was thus 21 (rounded down from 21.17), as seen in Table 8.

As ecological data (i.e. substrates and canopy level) was not analyzed in this study (which would normally require basic non-parametric statistics, as seen in Thorpe and Crompton 2005 and 2006), the only analysis conducted here is a comparison of percentages across studies, following Thorpe and Crompton (2009).

Some primate positional behaviour studies account for the violation of independence, in wild orangutan studies, visibility, as impeded by the canopy, omits sequential observation (Manduell et al., 2011). As such, following Thorpe and Crompton (2005), all postural and locomotor modes observed were analyzed.

## Chapter 4 – Results

### 4.1 Observation totals

Tables 5 and 6 summarize my observational and positional behavior totals by orangutan for each orangutan. Overall, the total time I spent observing focal individuals was roughly similar, except for Ulin and Tanjung. Ulin was still quite ‘wild’ compared to most other orangutans that ranged within the Prefab research area. During the days when we followed her, she displayed hiding behaviour and appeared unsettled by human presence. She was also being followed by 3 competing adult males, which may have further stressed her. As such, we could not follow her for more than 3 days. Tanjung is quite frequently found by local research assistants within the Prefab forest and is seemingly unbothered by human presence, but she spent many days interacting with her daughter, Bayur, and I collected ad libitum data on their interactions. A full data set analysis (which includes all individuals) can be found below, as well as a selective analysis of only Bayur and Labu’s positional behaviour data. This subanalysis will be used to compare adult female positional behaviour.

Table 5. Observation Totals by Individual

Name	Focal Days	Focal Minutes	Events	postural	locomotor
Labu pregnant	6	2598	428	196	232
Labu with Luna	5	2323	463	217	246
Bayur pregnant	8	3112	619	271	348
Bayur with Baby	9	3856	792	427	365
Langit	7	3069	410	235	174
Ulin	3	1028	98	34	65
Tanjung	1	29	20	9	11
Totals	39	16015	2830	1389	1441

Table 6. Focal Individual Totals by Behavioural Context

Individuals	Postural Events			Locomotor Events	
	Feed	Travel	Rest	Feed	Travel
Labu pregnant	105	44	47	51	181
Labu with Luna	157	27	33	41	205
Bayur pregnant	156	63	52	60	288
Bayur with Baby	314	74	39	100	265
Langit	202	18	15	46	128
Ulin	21	4	9	9	56
Tanjung	3	3	3	0	11
Totals	958	233	198	307	1134

## 4.2 All-individual data sets: interspecific (*P. abelii* and *P. p. morio*)

Tables 7 and 8 present the full data sets of all quantitative positional behaviour studies of orangutans conducted to date - Sugardjito and van Hooff (1986), Cant (1987a), Cant (1987b), Cant (unpublished data presented by Thorpe and Crompton in 2009), Thorpe and Crompton (2005, 2006, 2009), and the current study (2016). Credit for these tables is owed to Thorpe and Crompton (2009), who created and formatted them originally. I simply added my findings to them.

### 4.2.1. Postural modes

*Postures during rest.* The studies available for comparison of postural modes during *rest* are Sugardjito and van Hooff (1986) and Thorpe and Crompton (2009), both for *P. abelii*, and this study, for *P. p. morio*. Table 9 below highlights the most notable variations in relative frequencies.

The results for ‘sit’ during *rest* vary widely across studies. *P. p. morio* in the current study showed the highest frequency of sitting during *rest* by far (at a relative frequency of 72). *P. abelii* in Sugardjito and van Hooff study shows a result of 59, whereas *P. abelii* in Thorpe and Crompton’s present a result of 42. Similarly, relative frequencies vary widely for ‘lie’ during *rest*.

Table 7. Locomotor interspecific comparison: All-individuals (submode frequencies are subsets of mode frequencies)

	<i>P. abellii</i> <sup>1</sup>		<i>P. abellii</i> <sup>2</sup>		<i>P.p. morio</i> <sup>3</sup>		<i>P.p. morio</i> <sup>4</sup>	
	Travel (%)		Travel (%)		Travel (%)		Travel (%)	
	All	All	All	All	Adult Females	Adult Females	Females	Females
Quadrupedal & tripedal walk	12	15	24	12	12	16	21	45
Torso-orthograde suspensory locomotion	7 <sup>5</sup>	43	31	62	53	45	45	13
<i>brachiation &amp; forelimb swing</i>	19	16	12	11	9	16	32 <sup>6</sup>	7
<i>orthograde clamber &amp; transfer</i>		27	19	51	44	29	32 <sup>6</sup>	5
Bipedal walk		7	8	?	?	5	7	2
<i>bipedal walk</i>		2	2	0	0	3	5	2
<i>hand-assisted bipedal walk</i>	46	5	6	?	?	3	7	8
Torso-pronograde suspensory locomotion		3	5	1	2	7	5	2
Bridge		4	0	?	?	6	8	2
Vertical climb	11	12	18	12	19	8	8	2
Vertical descent		6	10	6	14	3	3	2
Sway	12	7	1	7	0	9	3	3

<sup>1</sup> Sugardjito and van Hooft (1986)<sup>2</sup> Thorpe and Crompton (2006)<sup>3</sup> Cant (1987a)<sup>4</sup> Current study (2016)<sup>5</sup> As per Thorpe and Crompton (2009), '?' demarks a difference in author classification systems and they were thus unable to quantify this mode<sup>6</sup> In both travel and feed for this mode, an 'unclear' torso-orthograde suspensory locomotion submode occurs at <1

Table 8. Postural interspecific comparison: All individuals (submode frequencies are subsets of mode frequencies)

	<i>P. abelli</i> <sup>1</sup>			<i>P. abelli</i> <sup>2</sup>			<i>P. abelli</i> <sup>3</sup>			<i>P. p. morio</i> <sup>4</sup>			<i>P. p. morio</i> <sup>5</sup>		
	Rest	Travel	Feed	Rest (%)	Travel (%)	Feed (%)	Rest (%)	Travel (%)	Feed (%)	Rest (%)	Travel (%)	Feed (%)	Rest (%)	Travel (%)	Feed (%)
	All	Adult Females	All	Adult Females	All	Adult Females	All	Adult Females	All	Adult Females	Adult Females	Females	Females	Females	Females
Sit	59	41	41	42	(47)	61	63	(62)	49	72	41	37			
Pronograde stand	3	26	2	0	(14)	14	4	(5)	<1	2	3	2			
Orthograde stand			17	0	(0)	6	7	(9)	2	4	9	6			
Orthograde-forelimb suspend				0	(0)	5	4	(7)		3	10	5			
Orthograde-forelimb suspend <i>one arm</i>			<1						<1	1	<1	3			
Orthograde quadrumanous suspend	4	33	other: 19	0	(0)	2	3	(3)	other: 11	4	12	17			
Forelimb-hindlimb suspend			ipsilateral: 14	0	(0)	7	12	(12)	ipsilateral: 30	6	21	29			
Pronograde suspend			other: 6.5	0	(0)	4	5	(5)	other: 6	0	<1	1			
Hindlimb-suspend			<1	0	(0)	0	1	(1)	<1	1	2	2			
Lie	34	0	0	58	(52)	1	1	(1)	0	10	<1	<1			

<sup>1</sup> Thorpe and Crompton (2009) calculated mean values for pauses during travel and rest for Sugardito and van Hooft (1986)<sup>2</sup> Cant (unpublished data), presented in Thorpe and Crompton (2009)<sup>3</sup> Thorpe and Crompton (2006). Adult female data presented in brackets<sup>4</sup> Cant (1987a)<sup>5</sup> Current study (2016)



*P. abelii* in Thorpe and Crompton has the highest relatively frequency at 58, and *P. abelii* in Sugardjito and van Hooff is 34, whereas in the current study *P. p. morio* was lowest at 10.

For ‘pronograde stand’ and ‘orthograde-quadrumanous suspend’ during *rest*, *P. p. morio* in the current study resembles *P. abelii* in Sugardjito and van Hooff most closely. For the remainder of the postural modes (‘orthograde stand’, ‘orthograde-forelimb suspend’, ‘forelimb-hindlimb suspend’, ‘pronograde suspend’, and ‘hindlimb suspend’), Sugardjito and van Hooff provide no relative frequencies for comparison, and Thorpe and Crompton’s results are all a relative frequency of zero. *P. p. morio*’s numbers here are the highest interspecifically. So, for both ‘sit’ and ‘lie’ during *rest*, the *P. abelii* findings appear to resemble each other more closely than they resemble the *P. p. morio* findings.

Table 9. Postural modes during *rest*:  
Relative frequency differences between previous studies and the current study

	<i>P. abelii</i>		
	Sugardjito & van Hooff <sup>2</sup>	Cant <sup>3</sup>	Thorpe & Crompton <sup>3</sup>
Sit <sup>4</sup>	^13		^30
Pronograde stand	-1		^2
Orthograde stand			^4
Orthograde-forelimb suspend			
Orthograde-quadrumanous suspend	0		^3
Forelimb-hindlimb suspend			^4
Pronograde suspend			^6
Hindlimb-suspend			0
Lie	-24		^1
			-48

<sup>1</sup>Data collected from Feb 1980-Dec 1982, published in 1986

<sup>2</sup>Unpublished data, presented in Thorpe and Crompton (2009) did not sample postural modes during *rest*

<sup>3</sup>Data collected from Dec 1998-Dec 1999, published in 2009

<sup>4</sup>^ denotes an increase in any study, - denotes a decrease in any study, 0 denotes that the numbers are equal

*Postures during feed.* The studies available for comparison for postural modes during *feed* are Cant (unpublished data, reported in Thorpe and Crompton (2009)) and Thorpe and Crompton (2009). Table 10 below highlights the differences in relative frequencies that are most notable.

For ‘sit’ during *feed*, *P. p. morio* in the current study resembles *P. abelii* in Cant’s study most closely (at relative frequencies of 49 and 41, respectively); *P. abelii* in Thorpe and Crompton is considerably higher at 63. Relative frequencies for ‘forelimb-hindlimb suspend’ in *P. abelii* are quite similar in Cant’s and Thorpe and Crompton’s studies, but more than double for *P. p. morio* in the current study. Relative frequencies for ‘orthograde quadrumanous suspend’ for *P. abelii* in Thorpe and Crompton are likewise very close to those in Cant but less than half the relative frequency for *P. p. morio* in the current study. The differences between *P. abelii* and *P. p. morio* for the remaining postural modes during *feed* are relatively low; ‘pronograde suspend’, and ‘orthograde stand’ being the greatest of these (at a relative frequency difference of 5 and 5.5, respectively).

Table 10. Postural modes during *feed*:  
Relative frequency differences between previous studies and the current study

	<i>P. abelii</i>	
	Sugardjito & van Hooff <sup>1</sup>	Cant <sup>2</sup> Thorpe & Crompton <sup>3</sup>
Sit <sup>4</sup>		-4 -26
Pronograde stand		0 -4
Orthograde stand		-5 -1
Orthograde-forelimb suspend		^1
Orthograde-forelimb suspend <i>one arm</i>		^3
Orthograde quadrumanous suspend		-2 ^14
Forelimb-hindlimb suspend		^15 ^17
Pronograde suspend		-5.5 -4
Hindlimb-suspend		^2 ^1
Lie		0 -1

<sup>1</sup> Data collected from Feb 1980-Dec 1982, published in 1986 and not sample postures during *feed*

<sup>2</sup> Unpublished data, presented in Thorpe and Crompton (2009)

<sup>3</sup> Data collected from December 1998-December 1999, published in 2009

<sup>4</sup> ^ denotes an increase in any study, - denotes a decrease in any study, 0 denotes that the numbers are equal

*Postures during travel.* The studies available for comparison are Sugardjito and van Hooff and Thorpe and Crompton. Table 11 below highlights the variations in relative frequencies that are most notable.

The greatest differences between *P. p. morio* and *P. abelii* are seen in ‘sit’, ‘pronograde stand’, ‘orthograde quadrumanous suspend’, and ‘forelimb-hindlimb suspend’. ‘Sit’ occurred at a

value of 20 higher for *P. abelii* in Thorpe and Crompton than for *P. p. morio* in the current study, but at the same frequency as *P. abelii* in Sugardjito and van Hooff. ‘Pronograde stand’ occurred at a value of 23 higher for *P. abelii* in Sugardjito and van Hooff than for *P. p. morio* in the current study, however, the difference is much smaller based on *P. abelii*’s results in Thorpe and Crompton.

For ‘orthograde quadrumanous suspend’, results for *P. abelii* in Sugardjito and van Hooff are more than double the result for *P. p. morio* in the current study (33 vs. 12), but higher than the value for *P. abelii* found by Thorpe and Crompton (2). And finally, ‘forelimb-hindlimb suspend’ is greater in *P. p. morio* in the current study than for *P. abelii* in Thorpe and Crompton (exceeding their result by 14) but no value is available from Sugardjito and van Hooff. The remaining postural modes during *travel* are quite similar between Thorpe and Crompton’s *P. abelii* and *P. p. morio* in the current study. The greatest of these differences is in ‘orthograde-forelimb suspend’, where *P. p. morio* in this study exceeds Thorpe and Crompton’s *P. abelii* by a relative frequency of 5.

Table 1.1. Postural modes during travel:  
Relative frequency differences between previous studies and the current study

	<i>P. abelii</i>	
	Sugardjito & van Hooff <sup>1</sup>	Thorpe & Crompton <sup>2</sup>
Sit <sup>4</sup>	0	-20
Pronograde stand	-23	-11
Orthograde stand		^3
Orthograde-forelimb suspend		^5
Orthograde-forelimb suspend <i>one arm</i>		
Orthograde quadrumanous suspend	-21	^10
Forelimb-hindlimb suspend		^14
Pronograde suspend		-4
Hindlimb-suspend		^2
Lie	0	-1

<sup>1</sup> Data collected from Feb 1980-Dec 1982, published in 1986

<sup>2</sup> Unpublished data, presented in Thorpe and Crompton (2009) (postures not sampled during travel)

<sup>3</sup> Data collected from December 1998-December 1999, published in 2009

<sup>4</sup> ^ denotes an increase in any study, - denotes a decrease in any study, 0 denotes that the numbers are equal

#### 4.2.2. Locomotor modes

*Locomotor modes during travel.* The studies available for comparison for locomotor modes during *travel* are Sugardjito and van Hooff (1986) and Thorpe and Crompton (2009). Table 12 highlights the greatest differences.

The only rather large difference is for ‘hand-assisted bipedal walk’, between *P. p. morio* in the current study and *P. abelii* in Sugardjito and van Hooff: 3 vs. 46. However, methodological differences may explain this, as Sugardjito and van Hooff included quadrumanous climb mode (Thorpe and Crompton, 2006); they found a value 43 higher than I did in this study. The other locomotor modes during *travel* are relatively consistent for *P. abelii* and *P. p. morio* based on the studies available.

Table 12. Locomotor modes during travel:  
Interspecific relative frequency differences between *P. abelii* studies and *P. p. morio* in the current study

	<i>P. abelii</i>	
	Sugardjito & van Hooff <sup>1</sup>	Thorpe & Crompton <sup>2</sup>
Quadrupedal & tripedal walk <sup>4</sup>	^4	^1
Torso-orthograde suspensory locomotion		^2
<i>brachiation</i> & <i>forelimb swing</i>	-3	0
<i>orthograde clamber</i> & <i>transfer</i>		^2
Bipedal walk <sup>3</sup>		-2
<i>bipedal walk</i>		^1
<i>hand-assisted bipedal walk</i>	-43	-2
Torso-pronograde suspensory locomotion		^4
Bridge		^2
Vertical limb	-3	-4
Vertical descent		-3
Sway <sup>3</sup>	-3	-2

<sup>1</sup> Data collected from Feb 1980–Dec 1982, published in 1986

<sup>2</sup> Data collected from December 1998–December 1999, published in 2009

<sup>3</sup> ^ denotes an increase in my study, - denotes a decrease in my study, 0 denotes that the numbers are equal

*Locomotor modes during feed.* The only study available for comparison for locomotor modes during *feed* is Thorpe and Crompton (2009); Sugardjito and van Hooft (1986) did not sample locomotor modes during feeding. Table 13 highlights the greatest differences.

Table 13. Locomotor modes during *feed*:  
Relative frequency differences between *P. abelii* and *P. p. morio* in the current study

	<i>P. abelii</i>	
	Sugardjito & van Hooft <sup>1</sup>	Thorpe & Crompton <sup>2</sup>
Quadrupedal & tripodal walk <sup>4</sup>		-3
Torso-orthograde suspensory locomotion		<sup>14</sup>
<i>brachiation</i> & <i>forelimb swing</i>		<sup>1</sup>
<i>orthograde clamber</i> & <i>transfer</i>		<sup>13</sup>
Bipedal walk <sup>2</sup>		-1
<i>bipedal walk</i> <sup>2</sup>		<sup>3</sup>
<i>hand-assisted bipedal walk</i>		-4
Torso-pronograde suspensory locomotion		<sup>2</sup>
Bridge		<sup>5</sup>
Vertical climb		-10
Vertical descent		-8
Sway <sup>2</sup>		<sup>2</sup>

<sup>1</sup> Data collected from Feb 1980-Dec 1982, published in 1986

<sup>2</sup> Data collected from December 1998-December 1999, published in 2009

<sup>3</sup> <sup>+</sup> denotes an increase in any study, <sup>-</sup> denotes a decrease in any study, <sup>0</sup> denotes that the numbers are equal

For ‘torso-orthograde suspend’, *P. p. morio* in the current study shows a value of 14 higher than *P. abelii*; most of this difference owes to the submode ‘orthograde clamber and transfer’. Based on the similar results for ‘vertical climb’ and ‘vertical descent’ for *P. p. morio* based on Cant’s findings, Thorpe and Crompton concluded that these postures are homogenous, interspecifically. However, for ‘vertical climb’, the *P. p. morio* value in the current study is half of what Thorpe and Crompton found in *P. abelii*. Similarly, ‘vertical descent’ was considerably less common (10 less) in *P. p. morio* during my study than in *P. abelii* during *feed*.

The rest of the locomotor modes during *travel* are relatively similar between the two species.

#### 4.3 *P. p. morio* interstudy comparison: Cant and Current Study

To enable comparison of *P. p. morio*'s positional behavioural in KNP now and approximately 35 years ago, I limited analysis of the current study's data to the two adult females only (Labu and Bayur, both when pregnant and not); Cant's study also assessed only two adult females. With this restriction, the sample sizes are quite similar, and both studies were conducted during powerful El Niño years. This comparison has the potential to confirm or negate the current picture of *P. p. morio*'s positional behaviour (as described most recently by Thorpe and Crompton). For this comparison, locomotor modes are presented during the behavioural contexts of *travel* and *feed*, and postural modes during the behavioural context of *feed* only (as Cant only sampled postural modes during *feed*). The results are summarized in Tables 14 and 15.

There are several differences between Cant's results and mine. It is of note that there are more differences in locomotor modes than there are in postural modes (in Table 15).

*Locomotor modes during travel.* My results show a dramatic reduction in 'torso orthograde suspensory locomotion', especially in the 'orthograde clamber and transfer' submode in particular. There is also an increase in 'torso pronograde suspensory locomotion' in my results.

*Locomotor modes during feed.* There are more differences seen in locomotor modes in *feed*. Values for 'quadrumanous tripedal walk' and 'torso pronograde suspensory locomotion' were higher in my study than in Cant's, and 'torso orthograde suspensory locomotion' (especially within the 'orthograde clamber and transfer' submode), 'vertical climb, and 'vertical descent' were lower. While Cant observed no instances of 'sway' during *feed*, this study observed a relative frequency of 3.

'Bipedal walk' occurred at 0 frequency in both *feed* and *travel* for Cant, but at 3 and 6 respectively in the current study. However, differences in methodology may affect this result and so interpretation ought to be done with caution. Cant stated that he observed 'bipedal walk' only when assisted by forelimbs, and classified this as 'orthograde clamber' (Thorpe and Crompton, 2009). As such, Thorpe and Crompton suggest that the 'hand-assisted' bipedal walk submode be examined in conjunction with Cant's 'orthograde clamber' result (2009). Thorpe and Crompton's compromise classification table, which I utilized for coding in this study defines 'bipedal walk' as unassisted when the forelimbs are in use but do not support more than their own weight.

However, when recording my data, I recorded ‘bipedal walk’ as unassisted when the forelimbs were not in use at all, a more stringent criterion. Implications are considered in the discussion section.

Table 14. Interstudy Comparison of Locomotor/positional Behaviour in KNP: Cant (1987a) & Current Study (2016)<sup>1</sup>

Locomotor Modes	<i>P. p. morio</i> 1982 <sup>2</sup>		<i>P. p. morio</i> 2015-2016 <sup>3</sup>		Differences <sup>4</sup>	
	Travel (%)	Feed (%)	Travel (%)	Feed (%)	Travel	Feed
<i>Adult Females</i>						
Quadrumanous/Tripedal Walk	12	12	16	22	^4	^10
Torso/Orthograde/Suspensory/Locomotion	62	53	44	43	-18	-10
<i>brachiation &amp; forelimb swing</i>	11	9	14	12	^3	^3
<i>orthograde/clamber &amp; transfer</i>	51	44	29	32	-22	-12
<i>unclear</i>	—	—	1	0		
Bipedal Walk	?	?	5	8		
<i>bipedal walk</i>	0	0	3	6	^3	^6
<i>hand-assisted bipedal walk</i>	?	?	2	2		
Torso/Pronograde/Suspensory/Locomotion	1	2	8	8	^7	^6
Bridge	?	?	6	5		
Vertical Limb	12	19	8	8	-4	-8
Vertical Descent	6	14	3	3	-3	-11
Sway	7	0	10	3	^3	^3

<sup>1</sup> Submode frequencies are subsets of mode frequencies

<sup>2</sup> Cant (1987a)

<sup>3</sup> Current Study (2016)

<sup>4</sup> ^ denotes an increase in the current study, - denotes a decrease in the current study, and 0 denotes equal values

*Postural modes during feed.* The biggest differences in results are for ‘sit’ and ‘pronograde suspend’, which both occurred at lower relative frequencies in the current study, and for ‘forelimb-hindlimb suspend’ which occurred at a higher frequency in my study. ‘Lie’ occurred at 0 in both studies during feed. The results for the remainder of the postural modes are broadly consistent between the two *P. p. morio* studies.

Table 15. Interstudy Comparison of Postural Positional Behaviour in *P. p. morio* (Cant 1987a) & Current Study (2016)<sup>1</sup>

Postural Modes	<i>P. p. morio</i> 1982 <sup>2</sup>	<i>P. p. morio</i> 2015-2016 <sup>3</sup>	Differences <sup>4</sup>
	Feed (%)	Feed (%)	
	2 Adult Females	2 Adult Females	
Sit	49	40	-9
Pronograde stand	<1	2	^2
Orthograde stand	2	5	^3
Orthograde-forelimb suspend		3	
	1 arm: <1	1 arm: 1	^1
Orthograde-quadrumanous suspend	other: 11	16	^5
Forelimb-hindlimb suspend	ipsi: 0	32	^2
Pronograde suspend	other: 6	0	-6
Hindlimb-suspend	<1	1	^1
Lie	0	0	0

<sup>1</sup>Submode frequencies are subsets of mode frequencies<sup>2</sup>Cant (1987a)<sup>3</sup>Current Study (2016)<sup>4</sup>^1 denotes an increase in the current study, ^2 denotes a decrease in the current study, and 0 denotes equal values

#### 4.4 Interspecific adult female comparison: *P. abelii* and *P. p. morio*

The individuals observed differed across studies, and as such, the results should be interpreted with caution. However, Thorpe and Crompton assessed a subset of their data for the adult females they sampled, so I have put combined this with Cant's and the current study's adult female data (see Table 16). This comparison may help clarify interspecific differences between *P. p. morio* and *P. abelii*, especially since the data sets are roughly similar across these studies.

Cant collected 1682 minutes of postural data on two adult females. The current study's results also represent two adult females, Labu and Bayur (while pregnant and not pregnant); 732 postural events during feed total, and approximately 2500 minutes of observation. Thorpe and Crompton's adult female data set is n=2515. This table was created only for postural modes, as Thorpe and Crompton (2005) had previously found that age-sex category has a weak effect on locomotor profiles and so only provided postural data for this subset in their 2009 publication.



Table 16. Adult female interspecific comparison<sup>1</sup>: Postural modes during the behavioural context of *feed*

	<i>P. abelii</i> T/C <sup>2</sup>	<i>P. p. morio</i> Cant <sup>3</sup>	<i>P. p. morio</i> Current <sup>4</sup>	Differences <sup>5,6</sup>		
	Feed (%) Adult Females <sup>6a</sup>	Feed (%) Two Adult Females	Feed (%) Two Adult Females	Cant vs. Current	T/C vs. Current	T/C vs. Cant <sup>6</sup>
Sit	62	49	40	-9	-22	-13
Pronograde stand	5	<1	2	^2	-3	-5
Orthograde stand	9	2	5	^3	-4	-7
Orthograde-forelimb suspend	4		3		-1	
Orthograde-one arm		<1	1	^1		
Orthograde-quadrumanous suspend	3	other: 11	16	^5	^13	^8
Forelimb-hindlimb suspend	12	ipsilateral: 30	32	^2	^20	^18
Pronograde suspend	5	other: 35	0	-6	-5	^1
Hindlimb-suspend	1	<1	1	^1	0	^1
Lie	1	0	0	0	-1	-1

<sup>1</sup>Thorpe and Crompton (2006): *n* = 2515 for their adult female data set, whereas *n* = 6524 for their entire data set<sup>2</sup>Thorpe and Crompton (2006) mean values for adult females, published in Thorpe and Crompton (2009)<sup>3</sup>Cant (1987a)<sup>4</sup>Current study (2016)<sup>5</sup>^ denotes an increase in the current study, ^- denotes a decrease, and 0 means the values are equal<sup>6</sup>a^ denotes an increase in Cant's findings, and ^- denotes a decrease in Cant's findings

Interspecific comparisons in Table 16 based on Thorpe and Crompton's *P. abelii* findings and my *P. p. morio* findings are relatively consistent with those in the all-individual interspecific comparisons (Table 10) above. Whereas Table 16 shows a difference of 22 for 'sit', the difference in Table 10 is 27. Similarly, other differences tend to be small: 'orthograde quadrumanous suspend' is 13 here, 17 in Table 10 and 'pronograde suspend' is 20 here, and 17 in Table 10. There are only marginal changes in interspecific differences for the remaining postural modes during *feed* based on this adult female and the all-individual interspecific table (Table 10).

Table 10 does show that interspecific differences between *P. abelii* and my results for *P. p. morio* are greater than the differences between Cant's and my results for *P. p. morio*.

#### 4.5 Dietary data: Cant and Current study

Cant also collected dietary data during his study, and as my data sheets were preformatted for dietary data, I was able to collect them as well with the help of the Project OK local research assistants. As Cant and I both conducted our studies during El Niño years – which can affect food availability and therefore ranging and postural behaviour – in the same national park, these dietary data are presented for comparison (see Table 17 and Figure 4, below).

The results show that fruit and flowers were consumed at the same relative frequencies. Bark consumption was slightly elevated for Cant, and leaf consumption was slightly elevated in the current study. There are small values for ants and termites in Cant’s study and an ‘unclear’ categorical value in the present study, generally due to the canopy obscuring visibility.

The main difference suggested by the dietary data results is that KNP’s females consumed slightly more bark and slightly less leaves in 1982 compared to 2015. Both high levels of bark and leaf consumption are considered to indicate poor food availability. While it is possible that the increased bark consumption displayed in 1982 indicates that forest conditions were worse during Cant’s study – it is also of note that KNP’s forest composition has changed substantially since 1982 (e.g., there are more pioneer than climax food species), and this may have contributed to the increased leaf consumption in 2015 (Russon et al., 2015).

Table 17. Dietary Comparison: Between 1982 and 2015 El Niño cycles<sup>1,2</sup>

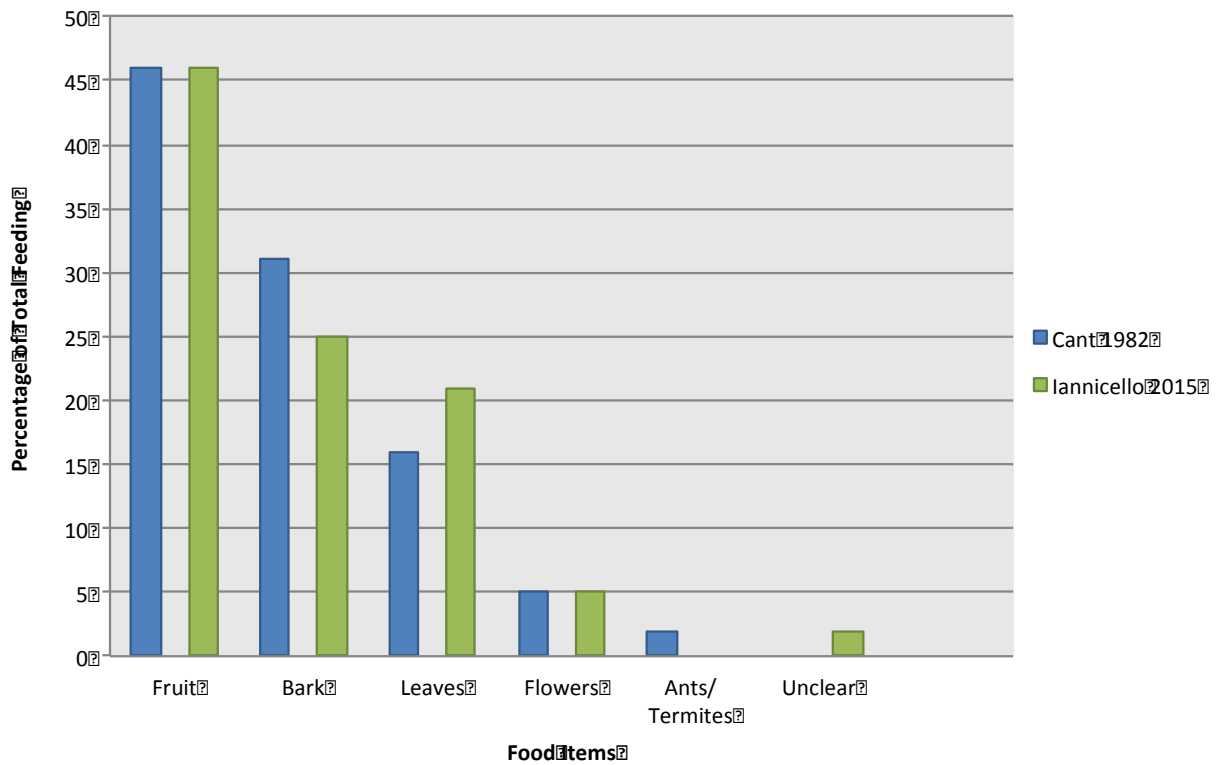
	Cant 1982 <sup>2</sup>	Iannicello 2015 <sup>3</sup>
Fruit	46	46
Bark	31	25
Leaves	16	21
Flowers	5	5
Ants/Termites	2	0
Unclear	0	2

<sup>1</sup> Numbers in this table represent the percentages of overall feeding time

<sup>2</sup> n=2665 minutes, Individuals are 22 adult females with offspring from August to November 1982

<sup>3</sup> n=2683 minutes, Individuals are 22 pregnant adult females during July 2015 and December 2015

**Figure 4.1 Dietary Comparison: Between 1982 and 2015 El Niños**



## Chapter 5 - Discussion

### 5.1 Interpretation of results

Replicating Cant's study in Kutai National Park in East Borneo provided a valuable opportunity to verify the current positional behaviour profile for the East Bornean orangutan subspecies, *Pongo pygmaeus morio*. Further, as the only other study on the positional behaviour of KNP's orangutans was done in 1982, this was not only an opportunity to corroborate interspecific comparisons between *P. abelii* and *P. p. morio* based on Cant's findings, but also an opportunity to examine how *P. p. morio*'s behaviour may have changed over time. KNP has long been subject to logging - both by concession and illegally, extensive mining, human encroachment, natural and human-fostered disasters, and various other activities that impact that wildlife within the park. The Bornean orangutan was recently upgraded to critically endangered by the IUCN and the activities in the park have only intensified over time. Replicating Cant's study on KNP's orangutans over 30 years later may then offer insight into the adaptive behaviour of a vulnerable species coping with precarious habitat.

That Cant conducted his study during an El Niño year is well known and often referred to in the positional behaviour literature as a limitation to the validity and legitimacy of his findings (Thorpe and Crompton, 2005, 2006, 2009; Myatt et al., 2011). A drought such as the one experienced in East Borneo in 1982-1983 has the potential to affect orangutan foraging patterns and ranging behavior severely (Thorpe and Crompton, 2009; Thorpe and Crompton, 2006; Manduelli et al., 2012; Phillips, 2011). In addition to the presumed limitation to his study caused by the drought, Cant was only able to sample two adult females for a short duration of only 4 months. So, in seeking interspecific comparisons, Thorpe and Crompton proceeded with caution because they conducted their study during a moderate La Niña year (Null, 2017), on all age-sex classifications, and for a long-term period of 13 months.

Conditions proved quite favorable to replicate Cant's study. I was able to conduct my study during an El Niño year, and a comparably short-term study was suitable for master's level research with limited resources. What was once a limitation to the positional behaviour data available on *P. p. morio* had become potentially quite valuable. The similarities between Cant's study and this study turned out unexpectedly strong - both conducted in KNP, presenting very similar data sets on two adult females (as well as a larger data set including more individuals),

both conducted during two out of the three “very strong” El Niño events by the National Oceanic and Atmospheric Association (NOAA) - 1982-83 and 2015-16 (the third being 1997-98) (Null, 2017). The fires often associated with El Niño events in Borneo were reportedly “exceptionally severe” in 2015 (Chen et al., 2016), and the 1982-1983 El Niño drought has been called a “fateful moment” in the lowland forests of Borneo (Dennis and Colfer, 2006). Finally, Cant’s study and the current study were conducted at very similar times of year; Cant collected data from August to November, whereas I collected data in July, December, and January. While these strikingly similar ecological conditions made for an opportune comparative study, they also mean that interspecific comparisons should be interpreted cautiously, since these interannual differences in ecology are likely to affect behavior.

NOAA data show that Thorpe and Crompton’s data collection period, from December 1998 to December 1999, was a ‘moderate’ La Niña year as of January 1999 (Null, 2017). Sugardjito and van Hooff’s (1986) positional behaviour data for *P. abelii* were collected between February 1980 and December 1982. NOAA data shows that while January 1980 is demarked as a ‘weak’ El Niño period, January 1982-1983 was, as we know, a ‘very strong’ El Niño event (Null, 2017). Essentially, the first year of Sugardjito and van Hooff’s data represents a very different type of year than their second year does, which again confounds interspecific comparisons. While Sugardjito and van Hooff’s field study area, Gunung Leuser National Park in Northern Sumatra (Indonesia), is affected by El Niño events that can be severe (e.g., 1997, 2006) and can result in serious drought and fire damage (Chen et al., 2016), ENSO events are reportedly worse in East Borneo (Qian, 2013). These factors limit comparability between El Niño events in North Sumatra and those in East Borneo’s Kutai National Park (Russon et al., 2015). Finally, methodological differences between Sugardjito and van Hooff (1986) and this study, e.g., our use of Thorpe and Crompton’s compromise classification table, suggests that the most reliable interspecific comparisons are perhaps with Thorpe and Crompton’s 2009 data.

## 5.2 Interspecific comparisons – *P. p. morio* and *P. abelii*

### 5.2.1. Support for interspecific conclusions found by Thorpe and Crompton (2009)

The results of my study support some of Thorpe and Crompton's (2009) interspecific conclusions based on Cant's findings for *P. p. morio* and their own *P. abelii* data. My data confirm that during feeding, *P. abelii* and *P. p. morio* exhibit the postural modes 'hindlimb suspend' and 'lie' at similar frequencies - both in adult females and across age-sex classes. My data also confirm that *P. abelii* exhibits 'pronograde stand' and 'orthograde stand' more frequently than *P. p. morio*, although marginally. Cant's unpublished data on *P. abelii* shows a higher value, but Thorpe and Crompton attribute this variation to methodological differences (2009). My study also confirms Thorpe and Crompton's conclusion that 'torso-orthograde suspensory locomotion' is the most prominent orangutan gait, and that *P. p. morio*'s use of locomotor modes 'orthograde clamber and transfer' is elevated - particularly during the behavioural contexts of feed and travel. Further, my data also supports the previous conclusion that 'brachiation and forelimb swing' (a submode of 'torso-orthograde suspensory locomotion') is similar for *P. abelii* and *P. p. morio* during the behavioural context of feed.

'Forelimb-hindlimb suspend'. Importantly, my results also confirm Thorpe and Crompton's 2009 conclusion that *P. p. morio* exhibits 'ipsilateral suspend' (a submode of 'forelimb-hindlimb suspend') far more frequently than seen in *P. abelii* (see Figure 5, below). Thorpe and Crompton argue that data on postures during travel would aid in clarifying whether or not the elevated use of this postural mode is specific to *P. p. morio*. My data appears to confirm that it is. Values for 'forelimb-hindlimb suspend' in *P. p. morio* are triple the value for *P. abelii* during travel. This may be among the most prominent evidence of interspecific positional difference between *P. abelii* and *P. p. morio*.

Thorpe and Crompton (2009) found that *P. p. morio*'s usage was more than double that of *P. abelii* during feed, based solely on Cant's data, and my data shows very similar results. And while it occurred during *rest* at zero in *P. abelii* for Thorpe and Crompton, it occurred at a value of 6 in *P. p. morio* in my study – a notable difference. This is especially important information, as this is the first time postural behaviour has been sampled on *P. p. morio* during *rest*. Furthermore, Thorpe and Crompton conducted a food type-positional behaviour analysis with Cant's *P. p. morio* data and found that bark is highly associated with 'forelimb-hindlimb

suspend', much more so than in *P. abelii*. A higher consumption of bark during Cant's study, as well as during this study, is attributable to the heavy reliance on bark as a fallback food during the El Niño caused drought (Thorpe and Crompton, 2009). Fallback foods are defined as: "foods of relatively poor nutritional quality and high abundance that are eaten when preferred foods are unavailable" (Harrison and Marshall, 2011, p. 532). It is also attributable to the heavy feeding on bark in Bornean orangutans; *P. p. morio* is known to have the highest bark consumption of all Bornean subspecies (Morrogh-Bernard et al., 2009).

Figure 5. Langit in 'ipsilateral hang', submode of 'forelimb-hindlimb suspend'



Photo Credit: Dedhy Irawan (2015) Research Assistant - Project OK

Moreover, during my data collection period, I observed several instances of ‘ipsilateral hang’ by post-natal Bayur and Labu. During this posture, the infant was able to rest on the side of their mother that was upwards facing. Essentially, it appeared to be a comfortable and safe place for the infant to rest its body while their mother paused during travel, rested, or fed (see Figure 6 below).

It is known that parous female orangutans tend to employ more caution in locomotion, more so than younger orangutans and adult males; this also appears to be associated with having offspring to care for as they travel (Thorpe and Crompton, 2005). This may suggest why Cant found similarly high levels of ‘ipsilateral hang’ in the two females he studied even though they did not have clinging infants; both did have accompanying offspring. Cant did not provide this information in his publication on positional behavior, but he observed the same individuals as Mitani (1989) did at roughly the same time period, and Mitani clearly states this information. Sugardjito and van Hooff (1986) also reported that female locomotion changed after parturition: females travelled at lower elevations, where substrate supports tend to be larger, and continued to do so even after their offspring assumed independence. This may suggest that the first parturition (the process of giving birth to an infant) is a transitional period in the behavioural profile of female orangutans (Thorpe and Crompton, 2005).

Figure 6. Labu in ‘ipsilateral hang’ with Luna



Photo Credit: Dedhy Irawan (2015) Research Assistant - Project OK



### 5.2.2. Divergences from previous interspecific findings

*'Brachiation and forelimb swing'*. Thorpe and Crompton found a different interspecific picture between *P. abelii* and *P. p. morio* in 2009 based on Cant's data. Cant's data found lower levels of 'brachiation and forelimb swing' than *P. abelii* in both travel and feed. My study, however, found this locomotor mode to be very close to *P. abelii* in both behavioural contexts (with only marginal differences seen). This is confirmed in both the all-individual data sets and the adult female-only data subset results (Table 14).

Using the support use data collected by Cant for *P. p. morio* and by Thorpe and Crompton for *P. abelii* – Thorpe and Crompton found, through log-linear analysis, that liana use was highly associated with 'brachiation and forelimb swing' in *P. p. morio*, and more so than in *P. abelii* (2009). While I did not analyze support use data, Bornean forests are known to have far more lianas than Sumatran forests (Thorpe and Crompton, 2009). KNP's abundance of lianas has been described as 'curtains' worth (Cant, 1987a). My own experience in KNP corroborates liana curtains. This supports interpretation of the higher value for 'brachiation and forelimb swing' found in the current study as more likely representing the amount of this locomotor mode employed by *P. p. morio* in KNP. Leighton and Wirawan (1986) found that approximately 90% of lianas died as a result of the 1982-1983 El Niño induced forest fires; this would likely have affected orangutan locomotion and thus perhaps rendered Cant's value for 'brachiation and forelimb swing' lower than found in the current study (after 20 years of forest regeneration since the fires of 1997-1998).

*'Sway' and 'bridge'*. My findings for 'sway' during feed and travel are higher than Cant's. This makes the similarity between *P. p. morio* and *P. P. abelii* greater than originally thought. Thorpe and Crompton (2009) concluded that oscillation during 'sway' is particularly fundamental to 'sway' in *P. abelii* as well as an interspecific functional difference between Sumatran and Bornean orangutans. This interpretation is consistent with Cant's reporting only rarely observing oscillations during 'sway' (1987a). Sugardjito (1982) and MacKinnon (1974) also report observing oscillation in Sumatran orangutans (2009). However, throughout my observation period, I personally observed to-and-fro oscillations by *P. p. morio* on several occasions, and Russon reports having observed oscillations during sway frequently in immature

Bornean rehabilitants (A. Russon, personal communication, March 1, 2015). Oscillation involves manipulating the compliance of the substrate; the individual uses their weight to oscillate the substrate (typically a slender, flexible tree) back and forth with increasing force to eventually propel themselves far enough to reach the desired tree and in effect bridge the gap in the canopy (Myatt et al., 2011). It is considered a key adaptation in orangutan travel (Myatt et al., 2011; Povinelli and Cant, 1995).

My observations were specific to Labu helping her juvenile daughter, Langit, cross particularly large gaps. Langit would enter the sway tree at a higher point directly above Labu, and Labu would use her weight to oscillate the tree and get them both across the gap simultaneously. Langit would then exit the tree before Labu, and Labu would follow. Presumably, Langit, with her much smaller body, may not have been heavy enough at the time to oscillate the tree on her own (Chappell, Phillips, and van Noordwijk, 2015) or to oscillate it as well or as far as needed. This is an example of maternal assistance, in which the offspring rides in the same tree its mother is swaying to reach the desired tree and cross a large gap. This is a well-documented form of maternal assistance (Bard, 1995), and it continues well into the period when the offspring starts to travel independently (van Noordwijk and van Schaik, 2005; van Noordwijk, et al., 2009). It also plays a crucial role in the offspring's slow development of locomotor ability through the examples provided by the mother (Bard, 1995).

Thorpe and Crompton (2009), through their log-linear analysis of support use and positional behaviour, found that *P. p. morio* does not employ lianas during 'sway'. While I did not analyze support use data, I can confirm that I did not observe liana swaying during my study.

Figure 7. Langit in position above Labu before ‘sway’ to cross a large gap

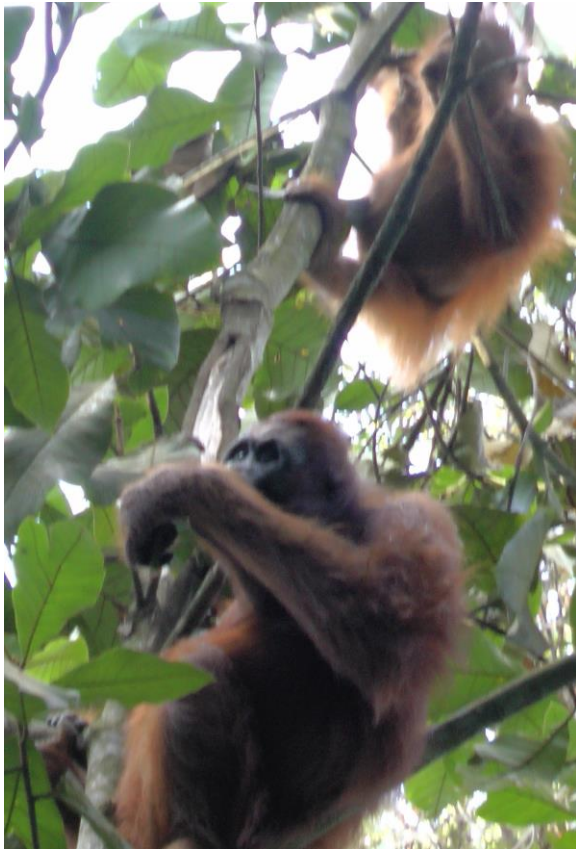


Photo Credit: Dedhy Irawan (2015), Research Assistant – Project OK

‘Bridge’ during feed occurred at an elevated rate in the current study in comparison to Thorpe and Crompton’s results for *P. abelii* (in fact, Thorpe and Crompton did not observe ‘bridge’ during feed at all). Due to methodological differences, there was no value provided for *P. p. morio* from Cant until now. In *P. p. morio*, this again may owe to the dynamic between Labu and her juvenile daughter Langit, since Langit was still dependent on Labu. I observed Labu frequently ‘bridging’ for Langit. When Labu and Langit encountered a particularly difficult gap, Labu would reach as far as she could to grab the terminal branches of the desired tree and pull them as close as possible, and then hold this position while Langit traversed the gap over the arboreal pathway created for her. Some instances also included Labu attempting to encourage Langit to cling to her back so to traverse a particularly large gap, but Langit would start to vocalize loudly and shake herself free of her mother’s grasp. In these instances, Labu would eventually resort to ‘bridging’ the gap in the canopy for Langit, grabbing the terminals ends of

the branches of the desired tree and bringing them close enough for Langit to cross. This is a well-documented form of active maternal assistance (Mackinnon, 1974). As such, this difference may perhaps be more closely associated with the mother-offspring dynamic than interspecific differences.

The maternal circumstances surrounding ‘forelimb-hindlimb suspend’ and ‘bridge’ are of importance because Thorpe and Crompton (2009) argue for “no clear evidence that higher levels of postural suspension found in *P. p. morio* are attributable to the study’s focus on females” (2009). My findings suggest that they might be.

*Bipedal Walk.* Thorpe and Crompton (2009) could not provide a value in their compromise classification table for ‘bipedal walk’ for *P. p. morio* based on Cant’s study, due to differences in classification and conflation of modes by Cant. However, Cant stated that he did not observe unassisted ‘bipedal walk’, so Thorpe and Crompton concluded there is no current evidence that *P. p. morio* employs the unassisted version of ‘bipedal walk’ (although they acknowledged that because orangutan gait is dominated by modes in which the torso is orthograde in orientation it is unlikely that they would never employ it). They also cite Davenport (1967) and MacKinnon (1974), who reported not observing any unassisted bipedal walking in Bornean orangutans.

An important distinction is that in Thorpe and Crompton’s compromise classification table, as a refinement from previous classification methodology, ‘bipedal walk’ (in juxtaposition to its submode counterpart ‘hand-assisted bipedal walk’, is assumed generally unassisted) could be recorded if the forelimbs were grasping substrates and not supporting more than their own weight. However, during the data collection period for the current study, I recorded unassisted ‘bipedal walk’ only when no forelimbs were aiding in movement in any capacity (there was no grasping of substrates). I only realized Thorpe and Crompton’s refinement well into my study. For this reason, I continued in the same manner that I had started throughout the remainder of the study for consistency. On that basis, I recorded a value for unassisted ‘bipedal walk’ of 5 during travel and 7 during feed during this study, which may be the first quantitative evidence of unassisted bipedal walking in *P. p. morio* to date.

The hands strictly free vs. hands grasping substrates but not holding their own weight specification did not apply to terrestrial locomotion, because terrestriality was noted but not analyzed systematically in this study. Regardless of how the focal individual moved terrestrially, it was noted, because significance lay in the fact that they came down from the trees - not in how they moved while on the ground.

*Terrestriality.* Bornean orangutans have no natural large predators, but Sumatran orangutans share their habitat with Sumatran tigers and for that reason are generally thought to travel very rarely on the ground (Thorpe and Crompton, 2009).

For a long period, reports for Bornean orangutan terrestriality were anecdotal, and most was attributed to adult males and less to females, especially females with offspring, as discussed above (Loken et al., 2013). Rodman (1979) reported that a flanged Bornean male spent approximately 20% of his locomotion time travelling terrestrially and Galdikas (1979) reported that a flanged Bornean male (*P. p. wurmbii*) moved terrestrially for long distance travels.

Rodman (1977), however, described observing 2 adult females on the ground in the Mentoko forest in KNP, and Campbell (1992) observed 3 instances of female terrestriality between 1985-1986 in the same location. More recently, camera traps in the Wehea Forest of East Kalimantan showed *P. p. wurmbii* females coming down from the trees to drink water and eat termites (Loken et al., 2013). Manduell et al. (2011) also reported female (*P. p. wurmbii*) terrestriality - finding that adolescent females travelled long distances terrestrially in Sabangau, Central Kalimantan, especially in disturbed forest areas.

While Cant (1987a) reported rarely seeing females travel outside the canopy in KNP, I personally observed two females (Bayur and Tanjung) coming to the ground rather frequently during the data collection for this study (see Figure 8, below). Tanjung moved terrestrially to travel between desired locations within the Prefab research site, and Bayur travelled terrestrially not only to change locations but also to obtain different foods. Interestingly, Bayur often came to the ground to breastfeed her newborn during the month of January of 2016 (her infant was born January 1st). This is the first time a wild individual, if I am not mistaken, has been directly

observed displaying this behaviour, and resting on the ground is considered uncommon in Bornean orangutans other than in flanged males (Ashbury et al., 2015).

Tanjung, Bayur's mother, has been a study individual for at least 30 years, according to a local research assistant who has worked at the Prefab for this duration and has encountered her frequently throughout this time. Further, it is highly likely Bayur became accustomed to human presence while dependent on her mother, and then even more so as she remained a study individual once independent. That said, Ashbury et al. (2015), recently suggested that habituation may not have as great an impact on terrestriality as previously assumed, as a study they conducted showed very little variation in terrestriality between habituated and unhabituated individuals (*P. p. wurmbii* in Central Kalimantan).

There are many speculations as to why Bornean orangutans may travel on the ground relatively frequently. Some consider that it provides recourse from falling due to breaking supports (Ashbury et al., 2015). This is a consideration for terrestriality in the individuals in this study as the forest was noticeably brittle during the study period, most likely because of the drought caused by the 2015-2016 El Niño. I also observed a few instances of branches and other supports breaking during orangutan arboreal travel, causing the individual to quickly adjust so as not to fall. This is an important consideration for orangutans: the largest and heaviest mammalian dwellers, they must consider their size as they travel through the canopy. Travelling on brittle supports incapable of supporting them means risking broken bones, contusions, and joint dislocations (Ashbury et al., 2015; Thorpe and Crompton, 2009; Kehoe and Chan, 1986). Another consideration is that while vertical displacement is energetically costly (Thorpe and Crompton, 2005), travelling terrestrially is quite cheap (Begun and Kivell, 2011; Cant 1987b). This consideration also fits well with the likelihood that quiescent (pregnant or lactating) females look to conserve energy.

As anthropogenic interference grows and fragmentation of orangutan habitat increases, the question many have begun to ask is how much habitat degradation is contribution to orangutan terrestriality (Ancrenaz et al., 2014; Loken et al., 2013; Rijksen and Meijaard, 1999). Manduella et al. (2011) proposed that that discontinuity in the canopy caused by selective logging might cause *P. p. wurmbii* to travel terrestrially, and this likelihood only increases in more heavily disturbed forest. Rayadin (unpublished data) also attributed terrestriality in *P. p. morio*

to anthropogenic disturbance, as he observed orangutans coming to the ground in fragmented forest patches as well as in acacia plantations and oil palm concessions to eat fruit (Loken et al., 2013).

Gauging behavioural flexibility and understanding how the behaviour of species changes in the face of disturbances, especially species that are endangered, may be a vital part of successful conservation planning for such a fragile species population (Ancrenaz et al., 2014). The data and observations of terrestriality in orangutans, Sumatran or Bornean, have important conservation implications. Conservation planning and policy must plan for terrestriality as it can also play an important role in human-orangutan conflict mitigation, which can arise as a product of orangutan terrestriality exacerbated by disturbance (Ancrenaz et al., 2014; McLennan and Hockings, 2016).

Figure 8. Bayur, with her clinging infant, travelling terrestrially at the Prefab

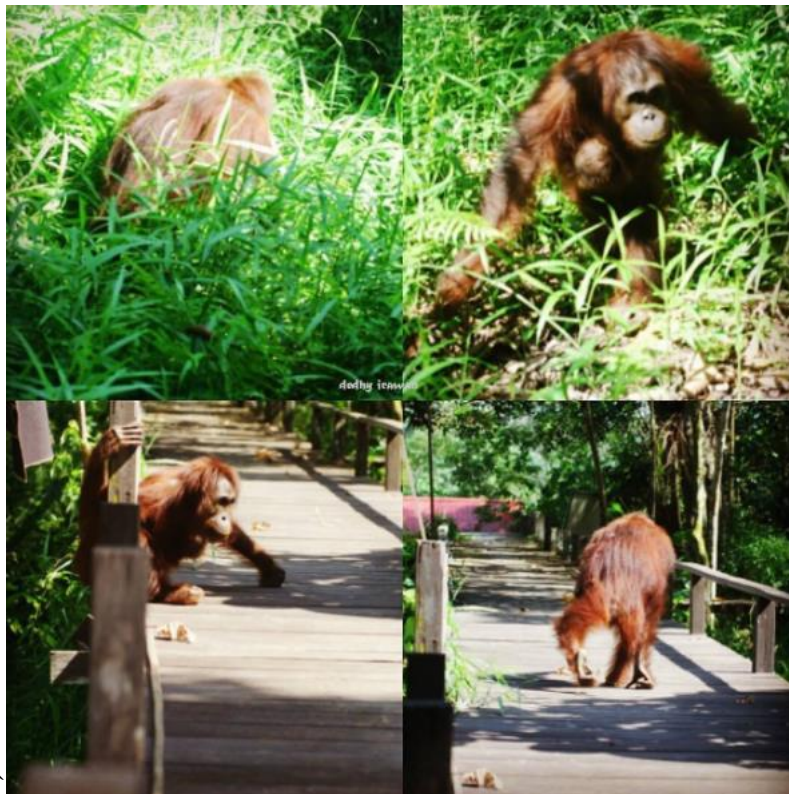


Photo Credit: Dedhy Irawan, (2015), Research assistant – Project OK

*Vertical climb* and *vertical descent*. Thorpe and Crompton concluded that *P. abelii* and *P. p. morio* were seemingly similar, interspecifically, in vertical climb and descent because their values and Cant's are strikingly similar. However, my findings differ widely from Cant's: they show a dramatically fewer instances of both locomotor modes, especially so during feed. During travel, my value is half of Cant's, and during feed, less than 15%.

A suggestion as to why Kutai NP *P. p. morio* values differ so much between 1982 and in 2015-2016 is that the adult females I observed were pregnant for at least half of my study period, whereas Cant's females were not (Mitani, 1989). Both locomotor modes are considered very costly, energetically (Thorpe and Crompton, 2005). Factoring in *P. p. morio*'s heavy reliance on bark as a fallback food, (especially because of the very strong 2015-16 El Niño), the increased feeding requirements of pregnant and lactating females (Mitani, 1989), and the fact that bark has especially low energetic return (Thorpe and Crompton, 2009), my very low values for vertical climb and descent may owe to my study individual's focus on energy efficiency in minimizing vertical displacement (Thorpe and Crompton, 2005; Isler and Thorpe, 2003).

### 5.3 Conservation implications of studying female individuals

While the prevailing view was once that orangutans are slow and cautious locomotors, especially adult females, they clearly, however, possess the capacity for great behavioural flexibility beyond this (Thorpe and Crompton, 2009). While adult females show the capacity for great caution and exceptional maternal care, they are also fierce ecological competitors and demonstrate acrobatic and fast locomotion. This latter type of locomotion has been described in the literature often in the context of aggressive encounters. Thorpe and Crompton (2006) described an adult displaying a costly and potentially dangerous locomotor behaviour when escaping an aggressive interaction which arose from competition over a favored food source. Rijksen (1978) provided a similar description of rapid movement in the context of fleeing an aggressive encounter. Female-female conflict may be a further pressure under which orangutans may be increasingly subject, given the trajectory of progressing orangutan habitat degradation and loss. Understanding this perhaps unforeseen stressor may illuminate important conservation implications for future conservation planning in KNP.



### 5.3.1. Female-female conflict

Females can clearly prioritize safety and caution, especially parous females (Thorpe and Crompton, 2005, Sugardjito and van Hooff, 1986). Aggressive encounters in adult females are generally considered quite rare, and of modest intensity. Aggressive encounters that escalate to physical violence are more likely seen amongst males (Marzec et al., 2016). The Tuanan research station in Central Kalimantan reported that only six female-female physical confrontations were observed in the Bornean subspecies *P. p. wurmbii* in 11 years (Marzec et al., 2016). It is well accepted that dominance relationships exist among adult male orangutans (Knott and Kahlenberg, 2007; Galdikas 1979, Utami Atmoko, 2000). Flanged males display dominance over unflanged males, often by supplanting them from trees with favored food source (Knott and Kahlenberg, 2007; Utami et al. 1997). Partly for that reason, physical confrontations are rare between flanged and unflanged males (Knott and Kahlenberg, 2007). Dominance relationships between adult female orangutans remains unclear (2007), but supplanting one another in fig trees has been described in adult females by Utami et al. (1997), which suggests a dominance relationships among adult females may occur (Knott and Kahlenberg, 2007).

However, within a three-month period, we witnessed 2 aggressive physical confrontations between adult *P. p. morio* females. Incidences involved Labu and Bayur, and the other Labu and Putri (a resident adult female of Mentoko, approximately 10 kilometers upriver).

Bayur, while physically smaller than Labu, appeared to be dominant over her. On several occasions, Labu retreated from and whined in Bayur's presence. Thorpe and Crompton (2006) similarly described an adult female, who, ranking lower in dominance to nearby females, would scramble down vertical substrates to avoid aggressive interactions when feeding. Bayur, on these occasions, appeared to tolerate Labu, and they remained in each other's vicinity (approximately 10 meters away), feeding in adjacent trees. On one occasion, however, Bayur leapt several meters into the tree in which Labu was feeding and attacked Labu until she fled by leaping out of that tree.

*Home ranges.* Females whose home ranges overlap are often matrilineally related (Arora et al. 2012, van Noordwijk et al., 2012), and females often show intolerance to females who share their home range but are not related to them (van Noordwijk et al., 2012). Bayur and Labu are not so related (as per long term research assistant information), but a 2014 study showed that

their home ranges do overlap (Ferisa et al., 2016), and so Bayur's intolerance of Labu may have escalated to physical aggression during this particularly difficult year in which Bayur needed to secure favored high caloric foods for energy for her and her newborn.

The increasing anthropogenic pressures encroaching on and within KNP's boundaries, then, might be affecting female home ranges, and potentially contributing to a rise in female-female conflict. Arora et al. (2012) reported an adult female being forced to shift her home range when pressures such as mining, logging and fires forced her out of her natural home range. She was reported to have avoided the females in her new home range, but was often chased by them when seen.

Studying female behaviour in difficult environmental conditions is then valuable for providing insights into behavioural flexibility, and how the death rate may increase within a species as a result of indirect pressure from anthropogenic pressures. Knowing the parameters and limits of this flexibility should advise and inform future conservation planning.

In July of 2014, a lethal female-female altercation was observed in Central Kalimantan (*P. p. wurmbii*) (Marzec et al., 2016). Notably, the home ranges of the females involved did not overlap. Putri, who is known to range in Mentoko and has been met by researchers there frequently since 2010, was attacked by Labu when Putri ranged into the Prefab area during this study. Labu spotted Putri from afar and chased her. Putri tried to flee but Labu caught her, grabbed the skin on her scalp, and tried to bite her. The pair crashed downwards through the canopy, breaking several branches. Langit retreated about 50 meters away and waited silently. Putri eventually fled. Both females were carrying their infants at the time.

So, while parous females demonstrate great capacity for strategic safety and emphasized caution, they are also capable of acrobatic and dangerous locomotor and behavioural profiles, and are willing to employ them, even while pregnant or with clinging infants, to secure resources in dire conditions.

### 5.3.2. Conservation Implications

Synchronicity between ecology and pregnancy has been observed in Bornean orangutans (Knott et al., 2009), which might explain Labu's and Bayur's synchronous pregnancies. Bornean females often become pregnant after an El Niño event ends, because of access to the high caloric intake provided by the fruit masting event that is triggered by the rainfall that ends an El Niño drought. Fruit production booms following the end of the El Niño drought for approximately 3 months (Russon et al., 2015; Knott et al., 2009). Orangutan caloric intake can be twice the normal intake during a fruit mast, and this spike in caloric intake and positive energy balance has been associated with pregnancy clusters (Knott, 1998). The reproduction of Sumatran orangutans is subject to different factors, as fruit availability throughout in Sumatra does not vary as greatly as it does in Borneo (Thorpe and Crompton, 2009).

However, the El Niño event of 2014 failed (Null, 2017) did apparently cause masting, resulting in Labu and Bayur becoming pregnant and giving birth during the successful El Niño of 2015-2016 and having to survive in the conditions of the resulting severe drought. Lactation is energetically costly (van Noordwijk et al., 2013), and a harsh environment that requires a reliance on fallback foods with poor energy return makes survival all the more difficult.

The function of aggression is often to secure limited resources (Wilson, 1975; Marzec et al., 2016), and as a rule in primates – “energy is limited, and food resources are subject to substantial competition” (Knott et al., 2009, p. 172). Considering the heightened reliance on fallback foods shown in *P. p. morio*, the magnitude of the El Niño event during this study, and the habitat fragmentation and degradation occurring in KNP, it is possible that the heightened intolerance of adult females shown to females outside their matrilineal lines, or with whom they do not share home ranges, is indicative of the importance of energy conservation for pregnant or lactating adult females.

The survival of females is an important consideration as they are impacted by habitat disturbances such as logging and the scarcity of food first and foremost; adult females often have accompanying dependents, are targeted by those looking to steal infants for the illegal wildlife trade, and are thought to be the first put at risk by food scarcity (Hardus et al., 2012). Female orangutans have also recently, contrary to what was commonly thought, been found to be more willing than their male conspecifics to exhibit risk prone behaviour as seen in their more frequent

crop raiding in Sumatra (Campbell-Smith et al., 2011). As such, studies that examine the way female orangutans adjust to difficult conditions have the potential to produce valuable information, which can help inform the crucial conservation planning.

## Chapter 6 - Conclusion

### 6.1 Summary

The purpose of this study was to observe and measure the positional behaviour of female Bornean orangutan of the subspecies *P. p. morio* in Kutai National Park, as well as to conduct interspecific comparisons with previously collected data for *P. abelii*, the Sumatran orangutan. The only other study of its kind on *P. p. morio* was conducted 35 years ago, and so this study presented an opportunity to re-assess the behavioural profile picture of *P. p. morio* as constructed by that sole study. Further, as the two studies in KNP were conducted during similar droughts, induced by El Niño events of the comparable magnitude, this study presented the opportunity to re-examine *P. p. morio* during a period of environmental disturbances, food scarcity, and heightened competition among adult females.

The findings of this study both confirmed and contradicted previous interspecific comparisons between *P. p. morio* and *P. abelii*. Specifically, this study confirmed *P. p. morio*'s elevated use of 'ipsilateral suspend', as well as its high association with bark consumption. This mode may be the most prominent evidence of interspecific differences.

This study's findings diverged from previous findings in 'brachiation and forelimb swing' and 'sway', showing higher use of these modes than previously found in *P. p. morio*, and show *P. p. morio* as more similar to *P. abelii* than originally found. And conversely, the results of this study found lowered levels of 'vertical climb' and 'descent' than previously found. This study also found several instances of terrestriality, which was not found by Cant (1987a), as well as instances of unassisted bipedal walking. Furthermore, this study filled certain knowledge gaps in interspecific positional behaviour. Whereas there were no data for *P. p. morio* postural behaviour during *rest* and *travel*, this study has now provided it.

Finally, this study found and described several instances of female-female conflict involving quick and acrobatic locomotor behaviour – demonstrating the capacity for a greater behavioural range than originally expected of orangutans, especially female orangutans. This behaviour appeared to be provoked by resource scarcity and difficult environmental conditions. This information may have important conservation implications, as understanding how critically endangered species react and adapt to disturbance, whether environmental or anthropogenic, may inform behavioural limits and adaptations (Hardus et al., 2012).

## 6.2 Limitations and recommendations

### 6.2.1. Limitations

This study was unable to analyze substrate data, which enables a more comprehensive understanding of orangutan behavioural ecology. Moving forward, measuring corresponding ecological data in KNP could enable verifying the findings Cant reported in 1987. Further, comparisons are complicated when sample sizes do not match. The differences in sample sizes and study individuals may have affected my comparisons. Moving forward, studies should seek to balance data sets as closely as possible.

### 6.2.2. Recommendations

*Intersite comparisons.* Thorpe and Crompton raised the question of whether the greatest differences exist at species or habitat level. Since ecological and habitat correlates undoubtedly affect orangutan behavioural profiles, positional behaviour and corresponding ecological and habitat use data should be collected to facilitate intersite comparisons for all orangutan species and subspecies.

*Climate change.* Climate change is a growing concern and has been found to exacerbate habitat destruction and loss (Boonratana, 2013; Ewers and Didham, 2006; Gregory et al., 2014). As such, studies moving forward should seek to measure the role of climate change in changing behavioural profiles and adaptations. Stuebig (2015) found that, based on climate projections, by 2080, 11-36% of Bornean mammals will lose over 30% of suitable habitat. Further, the IUCN recently identified the primate order one of the few orders likely to adapt quickly enough to climate change to survive (Schloss et al., 2012). Given the current immense pressures on KNP, both anthropogenically and environmentally driven, examining and predicting the ways in which climate change will further exacerbate habitat degradation and loss for *P. p. morio* is of paramount importance.

Climate change has also been identified as one of the key factors affecting species range shifts and distributions (Brown and Yoder, 2015). As the female-female conflict in KNP described here, as well as the fatal incident in Central Kalimantan (Marzec et al., 2016) may have escalated due to shifts in home range, factoring climate change into conservation planning

for the Critically Endangered Bornean orangutan may be crucial (Brown and Yoder, 2015). The ability to adapt and cope with habitat disturbance and range shift may be fundamental to survival. As such, studying the behaviour of a species on the brink of extinction may very well be essential to appropriate conservation planning and policy moving forward.

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# Appendices

## 1. Compromise classification table as it appears in Thorpe and Crompton (2009)

**Table 3.1** Compromise classification for positional behavior<sup>1</sup>

Positional behavior
<p><b>Postures</b></p> <p>Sit: Includes all sit submodes in Thorpe and Crompton (2006).</p> <p>Pronograde stand: Standing on 3 or 4 limbs with the torso pronograde (—). Cant (1987a) only observed 'tripodal stand' as 1 forelimb was involved in feeding. Sugardjito and van Hooff (1986) combined pronograde and orthograde stand.</p> <p>Orthograde stand: Standing on 1 or 2 legs with the torso orthograde ( ). Equates to Cant's (1987a) 'bipedal stand'.</p> <p>Orthograde forelimb-suspend: Torso-orthograde suspensory postures with body mass supported by forelimbs only. Cant (1987a) only observed single forelimb-suspend ('one-hand hang'). Sugardjito and van Hooff (1986) combine all suspensory postures under a single 'hanging' mode.</p> <p>Orthograde quadrumanous suspend: Orthograde suspension with body mass borne by forelimbs and hindlimbs in suspension. 'Trunk-vertical hang' in Cant's (1987a).</p> <p>Forelimb-hindlimb suspend: Hanging by a forelimb and hindlimb on the same (ipsilateral) or opposite (contralateral) side of the body. Cant (1987a) specifies ipsilateral suspend ('hand-foot hang 1'), but combines contralateral suspend, pronograde suspend and hanging by one hand and both feet ('hand-foot hang 2'). Thorpe and Crompton (2006) did not observe the latter.</p> <p>Pronograde suspend: Inverted pronograde suspension using hindlimbs and forelimbs.</p> <p>Hindlimb suspend: Hanging upside down, by one/both feet. 'Foot-hang' in Cant (1987a).</p> <p>Lie: Not observed by Cant (1987a) during feeding.</p> <p><b>Locomotion</b></p> <p>Quadrupedal and tripodal walk: Includes regular and irregular quadrupedal and tripodal gait. Cant (1987a) did not observe irregular gait walk (pronograde scramble).</p> <p>Torso-orthograde suspensory locomotion: Suspensory locomotion with the body orthograde. Body mass is mainly supported by the forelimbs. Sugardjito and van Hooff (1986) separate brachiation but classify all remaining suspensory locomotion as 'quadrumanous scrambling'. Here I separate submodes in which the forelimbs bear all body mass (brachiation and forelimb swing) and those in which the forelimbs bear the majority of mass, but the hindlimbs support &gt;their own weight (orthograde clamber and transfer). The latter equates to Cant's (1987a) horizontal and diagonal clamber.</p> <p>Bipedal walk: Hindlimbs provide the majority of support and propulsion. Includes hand-assisted (where forelimbs support &gt;their own mass in suspension or compression), and unassisted forms. Cant (1987a) only observed hand-assisted forms, which he classified as orthograde clamber. 'Hand-assisted bipedal walk' should therefore be viewed in association with orthograde clamber for comparative purposes.</p> <p>Torso-pronograde suspensory locomotion: Suspensory locomotion with the torso pronograde. 'Inverted quadrupedalism' in Cant (1987a). Combined with torso-orthograde suspensory locomotion by Sugardjito and van Hooff (1986).</p> <p>Bridge: A torso-pronograde gap crossing movement.</p> <p>Vertical climb: Cant (1987a) defined vertical climbing as ascent within 22.5° of true vertical. Thorpe and Crompton (2006), following Hunt <i>et al.</i> (1996), defined vertical climbing within 45° of true vertical, but provided frequencies for true vertical (0–20°) and angled climb (20–45°) separately since Thorpe and Crompton (2005) argued that angled climb should be included in the submode 'orthograde clamber'. Here vertical climb refers to locomotion within approximately 20° of true vertical and angled climb is included in 'orthograde clamber and transfer'. Sugardjito and van Hooff (1986) do not provide an angular distinction between vertical climb and quadrumanous suspend.</p> <p>Vertical descent: Classification follows restrictions as detailed for vertical climb</p> <p>Sway: Oscillatory locomotion including tree sway and swinging on vertical branches and lianas in a 'tarzan' style. Cant (1987a) and Sugardjito and van Hooff (1986) only documented tree sway.</p>

<sup>1</sup>All classifications are based on Thorpe and Crompton (2006).

[illegible]

Lokasi: \_\_\_\_\_  
Cuaca: \_\_\_\_\_